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SOME PARASITIC NEMATODES FROM MAMMALS OF SOUTH CHINA

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(With 22 Figures in the Text)

THE following is a report on a collection of four species of parasitic nematodes from some mammals of Kwangtung Province, South China.

Rictularia mjöbergi Baylis, 1928
(Figs. 1–6)

Five females and two males of this species were available for study. The male is described for the first time.

Specific description. Stout worms, with the body generally bent ventrally and rarely dorsally. Cuticular striations distinct. Mouth directed dorsally. Head provided with two circles of papillae, the inner circle consisting of two subdorsal, relatively close together, and two subventral, farther apart. A pair of indistinct bodies probably represent the lateral papillae. The outer circle consists of four papillae situated submedially. Mouth guarded by a transverse row of small teeth directed anteriorly. Wall of buccal capsule heavily chitinized and thicker on the ventral side. From the base of the capsule there arise three tooth-like projections, that in the middle being situated on a transverse ridge as seen in dorsal view. Two rows of subventral cuticular "combs" and spines extend throughout almost the whole length of the body, their number varying according to sex.

Male. Because of the very much bent condition of one of the worms, the measurements and description, unless otherwise stated, were based on the larger specimen only.

The size of the two males is $4{\cdot}3 \times 0{\cdot}259$ mm. and $6{\cdot}91 \times 0{\cdot}468$ mm. respectively. The posterior end is characteristically curled. There is a slight cuticular expansion from the dorsal aspect at the anterior end to about the seventh pair of subventral "combs". From the lateral aspect a distinct cuticular expansion can be seen in the region of the first two or three subventral "combs" and then gradually disappears at the level of the sixth subventral "combs". In the smaller specimen, however, a very wide cuticular expansion (0·0645 mm.) can be seen on the ventral side, beginning at the head and extending almost to the region of the eighth subventral "comb", while on the dorsal side there is a slight cuticular expansion less than half the length of the ventral one. Cuticular striations 8–22 μ apart. Width of head at base

of buccal capsule 0·126 mm. Buccal capsule 0·067 mm. wide at base. Oesophagus 2·56 mm. long. Cervical papillae 1·47 mm. from anterior end of body. Spicules unequal, 0·319 and 0·118 mm. long. In spite of the difference

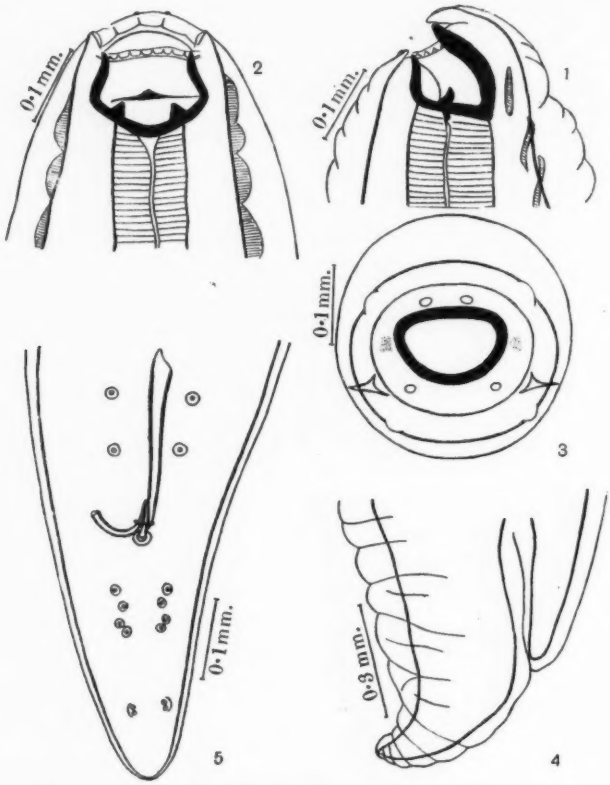


Fig. 1. *Rictularia mjöbergi*, lateral view of the anterior end of a female, showing the buccal capsule, the position of the oral aperture, and the position of the first "combs" in relation to the buccal capsule.

Fig. 2. *R. mjöbergi*, dorsal view of the anterior end of a female, showing the buccal capsule, the tooth-like projections and the circumoral teeth.

Fig. 3. *R. mjöbergi*, front view of the anterior end of a female, showing the cephalic papillae, and the first pair of cuticular "combs".

Fig. 4. *R. mjöbergi*, lateral view of the posterior end of a female, showing the anus.

Fig. 5. *R. mjöbergi*, ventral view of the posterior end of the larger male, showing the position of the caudal papillae and the spicules.

in size between the two specimens, the spicules are remarkably uniform in size. There is a heavily chitinized structure, somewhat irregular in shape, at the posterior end of the spicules. This is apparently a gubernaculum, and is 0·035 mm. long. The caudal papillae consist of two pairs of pre-anal and five

pairs of post-anal. Of the latter the most posterior pair are situated at some distance from the rest and have double terminations. Tail 0·223 mm. long.

There are sixty-five or sixty-six pairs of subventral "combs" and spines. The first pair somewhat overlaps the middle of the buccal capsule. All of them, particularly towards the extremities, are rather close together. The last pair is 1·176 mm. (in the smaller specimen 0·750 mm.) from the posterior end of the body. Four or five median ventral "combs" are present, the last a short distance in front of the cloaca and the first overlapping the region of the last one or two pairs of subventral spines. They are somewhat different in size, becoming progressively larger posteriorly.

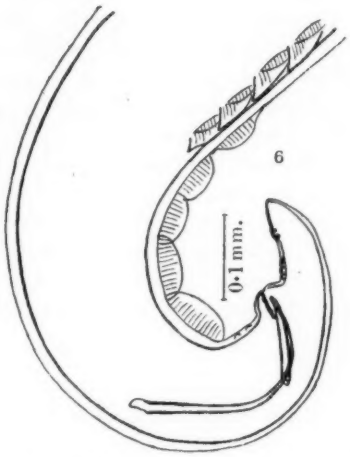


Fig. 6. *Rictularia mjöbergi*, lateral view of the posterior end of the smaller male, showing spicules, gubernaculum, median "combs" and the characteristic inrolling of the tail.

Female. The body varies from 25 to 35 mm. in length and 1·1 to 1·4 mm. in greatest diameter. Cuticular striations about 10–36 μ apart, the distance between them increasing towards the posterior part of the body. Buccal capsule 0·122 mm. wide at base. Width of head at base of buccal capsule 0·245 mm. Oesophagus 6·6 mm. long. Nerve-ring 0·58 mm. and cervical papillae 1·14 and 1·2 mm. from anterior end. Vulva inconspicuous, 1·84 mm. behind oesophagus, the vagina being directed posteriorly. Tail 0·504 mm. long, somewhat curved. Eggs oval, 43 by 25 μ.

There are ninety to ninety-two pairs of subventral "combs" and spines, the first pair at the level of the middle of the buccal capsule and the last pair at about 3·8 mm. from the posterior end. Forty-five or forty-six pairs of "combs" are pre-vulvar. Distinct spines are found posterior to the vulva. The first fifty to sixty pairs are rather close together, the most anterior even overlapping one another. They become farther apart posteriorly.

Host. Paguma larvata larvata H. Smith.

Location. Small intestine.

Locality. Kwangtung Province, China.

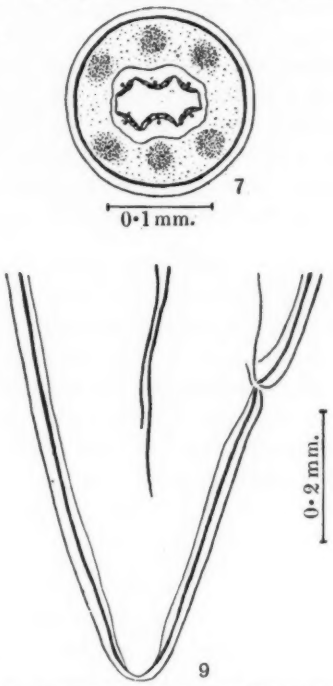
Discussion. The female of this species was first described by Baylis (1928) from *Arctictis binturong* from Sarawak. Sandground (1933) described a new species, *Rictularia wheeleri*, from *Paguma larvata intrudens* from Lai Chau, Tonkin, and his description was based also on females. A careful comparison of the two species indicates that they are very similar in morphology and therefore *Rictularia wheeleri* may fall as a synonym of *R. mjöbergi*. The present worms differ from those originally described by Baylis in the fact that Baylis's specimens have ninety-four to ninety-seven pairs of subventral cuticular "combs" and spines, of which forty-seven to forty-nine are situated in front of the vulva, and moreover, the first pairs are not located at the level of the buccal capsule. *R. wheeleri* does not agree with the present specimens in the fact that the cervical papillae are anterior to the nerve-ring, the tail is much shorter, the eggs are smaller, and the number of subventral cuticular "combs" and spines is about 100. Since many of these variations are found even among individuals collected from the same host and since both Sandground and the present writer have not had sufficient specimens to establish a sufficient range of variation, I regard the present specimens as belonging to *R. mjöbergi* and *R. wheeleri* as a possible synonym of the latter. Table I gives a summary of the characters of Baylis's, Sandground's and the present specimens.

Table I. *A comparison of the specimens of Baylis, Sandground, and present author (females only)*

	R. mjöbergi Baylis, 1928	*R. wheeleri* Sandground, 1933	Present specimens
Size	25–60 × 0·9–1·6 mm.	38 × 1·45 mm.	25–35 × 1·1–1·4 mm.
Oesophagus	Distance from anterior end to end of oesophagus 4·5–6·0 mm.	5·0–5·2 mm. long	6·6 mm. long
Nerve ring from anterior end	0·45–0·6 mm.	0·57 mm.	0·58 mm.
Cervical papillae from anterior end	0·7–1·0 mm.	Anterior to nerve ring	1·137–1·224 mm.
Buccal capsule to anterior margin of first "combs"	—	0·51 mm.	Overlapping the first "combs"
Vulva	1–1·4 mm. behind oesophagus or at 47th to 49th "combs"	1·95–2 mm. behind end of oesophagus	1·84 mm. behind oesophagus or at 45th or 46th "combs"
"Combs"	94–97 pairs altogether: 47–49 pre-vulvar; cease at some considerable distance from posterior end	100 (±5) pairs: 50 (±1) are anterior to vulva. Last pair 5·98 mm. from posterior end of body	92 pairs: 46 pre-vulvar. Last pair 3·8 mm. from posterior end
Eggs	47 × 32 μ	Largest 36·2 × 25·3 μ	43 × 25 μ
Tail	0·45–0·55 mm.	0·195 mm.	0·504 mm.

Ascarops dentata (Linstow, 1904)
(Figs. 7–9)

This species was collected from the stomach of hogs (*Sus scrofa domestica*) slaughtered in Canton, and infected 29 per cent of the hogs examined. It was tentatively identified (Chen, 1936) as *Ascarops* sp. (=*Arduenna* sp.), with the intimation that it might be *A. dentata*. Upon more careful study I have found that the specimens actually belong to that species, but there are many



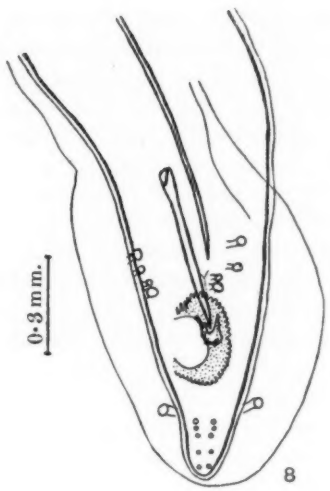


Fig. 7. *Ascarops dentata*, front of the head of a female, showing cephalic papillae and the two trilobed lips.

Fig. 8. *A. dentata*, ventral view of the posterior end of a male. Note the spicules, gubernaculum, pericloacal crown, papillae and caudal alae.

Fig. 9. *A. dentata*, lateral view of the posterior end of a female.

technical points which require further elucidation, hence the following detailed description.

Specific description. Filiform nematodes, whitish in colour. Cuticle finely annulated transversely throughout length of body in both sexes. In male, annulations replaced by serial rows of elongate thickenings on ventral side, slightly anterior to the longer spicule. Six large cephalic papillae present. Length of oesophagus one-sixth total length in male, one-ninth in female. Caudal wing in male tightly and characteristically inrolled. Tail of female straight and bluntly conical.

Male. Body 25–30 mm. long, with maximal breadth of 0·73 mm. Pharynx 0·086 mm. long and 0·04 mm. wide, with walls 0·01 mm. thick. Oesophagus with slender anterior portion 0·43 mm. in length; longer and wider posterior portion 4·14 mm. in length. Nerve-ring 0·46 mm. from anterior end, encircling anterior portion of oesophagus. Excretory pore 0·59 mm. from anterior end. Cervical papillae asymmetrical in position, the right 0·7 mm., the left 0·3 mm. from anterior end. Cervical ala begins on left side of body near nerve-ring, and extends caudad 4·86 mm.; its greatest width 0·03 mm. Spicules dissimilar and unequal, the left 4·1 mm. long, 0·02 mm. wide at base, and having a pointed tip; the right 0·6 mm. long and 0·036 mm. wide, with a barbed tip. Gubernaculum heavily chitinized, somewhat V-shaped, within the pericloacal crown. Pericloacal crown, on left side, a semilunar band of cuticle with serrate edge, length 0·315 mm. and width 0·22 mm. Anus 0·504 mm. from posterior end of body. Caudal alae asymmetrical, the left 1·47 mm. long and 0·28 mm. wide, the right slightly longer and much narrower. Width across caudal alae in cloacal region 0·88 mm.

Left ala covered ventrally by serial rows of elongate thickenings, and right by scale-like thickenings of cuticle. Alae supported by five pairs of pedunculated papillae and five pairs of inconspicuous, apparently sessile, papillae. Former divided into four pre-anal pairs, asymmetrical in position, and one post-anal pair. First three pre-anal pairs almost equidistant and fourth pair close to third. Sessile papillae located on smooth area towards extremity of ventral surface of tail, three pairs close together, tandem, one a little distance towards the tip of the tail and the last near the tip.

Female. Body 43–55 mm. long and approximately 1 mm. in maximal breadth. Pharynx 0·182 mm. long, 0·05 mm. wide, with walls 0·012 mm. thick. Oesophagus, narrow anterior portion 0·49 mm. long, posterior part 5·32 mm. long. Nerve-ring encircles narrow portion of oesophagus 0·485 mm. from anterior end of body. Excretory pore 0·59 mm. from anterior end. Cervical papillae asymmetrical in position, the left 0·32 mm., the right 0·664 mm. from anterior end. Cervical ala begins on left side of body near nerve ring, and extends caudad 12·64 mm.; its greatest width approximately 0·04 mm. Vulva very inconspicuous, in the anterior two-fifths of the body, immediately behind a slightly swollen area. Anus very conspicuous, 0·58 mm. from posterior end. Width of anal region 0·398 mm. Eggs 0·036 by 0·022 mm., numerous and apparently embryonated *in utero*.

Discussion. The genus *Ascarops* was first established by van Beneden (1873) for certain nematode larvae encysted in the stomach wall of a bat in Belgium. Ono (1932) has reported the recovery of *Arduenna strongylina* from a rabbit fed with encysted larvae from a bat. This was later confirmed by Alicata & McIntosh (1933), who believed that the larvae found by van Beneden, Ono and themselves are all the same and that therefore the name *Arduenna* should fall as a synonym of *Ascarops*.

There are in the foregoing description some apparent differences between

the present specimens and those studied by von Linstow (1904). In the first place, in the original description by von Linstow the spicules are 0·35 and 0·92 mm. long, respectively, which is much shorter than those of our specimens. It seems quite possible that von Linstow's measurement is not entirely correct. Indeed, Railliet & Henry (1911) did not hesitate to identify their specimens as *A. dentata*, although their spicules were much longer than those of von Linstow's specimens, and agreed closely with the measurements given for our specimens.

In the second place, there is some discrepancy as to the position of the vulva. We have found it to be anterior to the middle of the body, while von Linstow states that it is behind the middle of the body. Since the opening is rather inconspicuous, von Linstow may have taken something else for the vulva. It is interesting to recall in this connexion that Railliet & Henry failed to locate the vulva in their specimens, and this makes it more likely that von Linstow did not see the real vulva.

Lastly, there may be a question as to the presence or absence of the gubernaculum. Von Linstow did not describe it, neither did Railliet & Henry. In our own specimens, however, we did not have much difficulty in seeing the structure. It seems possible that the previous workers had overlooked its presence.

For the above reasons I have assigned my specimens to *A. dentata*.

Pseudophysaloptera soricina Baylis, 1934
(Figs. 10–16)

About two dozen specimens of this species were collected from the stomach of local shrews, *Suncus coerulus*. They are, as a rule, found with their anterior ends embedded in the stomach-wall of the host. The species was first described from the stomach of an African shrew (*Crocidura* sp.) by Baylis (1934). Since more material is available for study and since a great many variations are found between the Asiatic and the African forms, a detailed description is herewith given for comparison, as well as for the elucidation of some structures not clearly seen previously.

Specific description. Body stout and characteristically bent. Cuticle thick, greatly wrinkled here and there, generally inflated from near the level of the junction of the anterior and posterior parts of the oesophagus, and reflected over the lips to form a more or less distinct cephalic collarette. Cuticular striations in male very fine and may easily be overlooked; in female, often not discernible. Head bears two large lateral lips, with the inner face flattened and the outer face convex. Inner margin of each lip provided with three notched teeth, and its dorsal and ventral sides may sometimes be denticulated. Six large cephalic papillae present, two laterally and four submedially. Mouth cavity small and vestibule absent. Oesophagus long and divided into two

portions; anterior portion narrower, shorter and muscular and posterior portion longer, wider and glandular, the increase of diameter being gradual. Cervical papillae small and inconspicuous. One or more cuticular expansions of

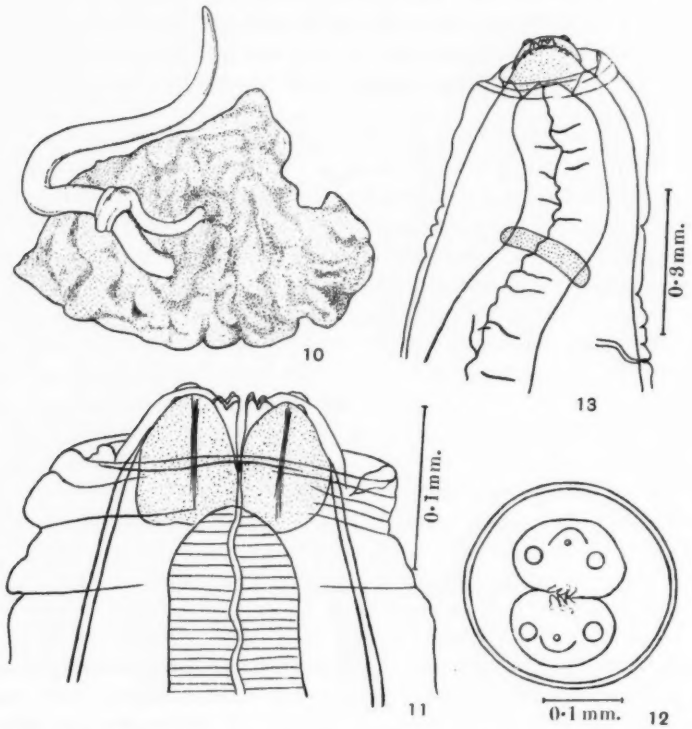


Fig. 10. *Pseudophysaloptera soricina*, a free-hand drawing based on observations under a Greenough binocular. The sketch shows copulation, the anterior ends of the worms being embedded in the mucosa of the stomach wall at the same time. It is not possible to show in the sketch exactly how far the anterior ends of the worms are embedded in the tissue, since the stomach wall is not smooth.

Fig. 11. *P. soricina*, dorsal view of the anterior end of a male, showing the cephalic collarette, the two large lips and the notched teeth.

Fig. 12. *P. soricina*, front view of the head of a female, showing the cephalic papillae and the notched teeth.

Fig. 13. *P. soricina*, lateral view of the anterior end of a female, showing nerve-ring, excretory pore, lips, teeth, cephalic collarette and anterior cuticular expansions.

various sizes usually present on any part of body. Male: tail characteristically coiled towards the ventral side and apparently provided with numerous sessile caudal papillae. Female: body characteristically constricted ventro-laterally in anterior third or fourth, or rarely fifth, of total body length.

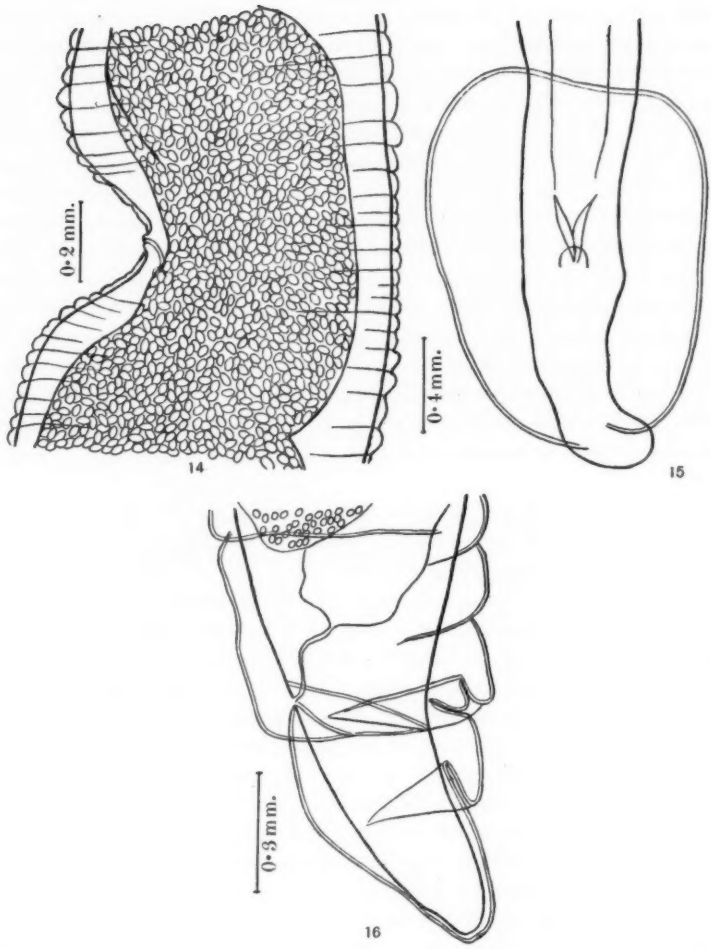


Fig. 14. *Pseudophysaloptera soricina*, constricted area in the region of the vulva. The anterior end is above.

Fig. 15. *P. soricina*, ventral view of the tail of a male, showing the caudal alae. The spicules are in the middle. Caudal papillae are not observed in this particular specimen.

Fig. 16. *P. soricina*, lateral view of the tail of a female, showing cuticular expansions and wrinklings, and the anus.

Male. Body 0·524 mm. in greatest diameter and 8·73 mm. long, often sharply bent dorsally at middle or towards anterior end of body, or occasionally spirally coiled. One or more large dorso-lateral, ventral, or dorsal cuticular expansions present between caudal alae and anterior end of body. Cephalic collarette 0·185 mm. in diameter. Lips 0·072 mm. high and 0·072 mm. wide at base. Cervical papillae 0·608 mm. and nerve-ring 0·386 mm. from anterior end of body. Excretory pore 0·633 mm. from anterior end of body, its duct leading obliquely forward. Oesophagus 2·75 mm. long, anterior portion being about 0·38 mm. long. Diameter of anterior portion of oesophagus at anterior tip 0·073 mm. and of posterior portion at base 0·162 mm. Spicules (?) indistinct, in the form of two barely discernible structures, equal, pointed at both ends, 0·15 mm. long. Gubernaculum absent. Papillae generally not observed; when seen they are minute, numerous, sessile, and irregularly and subventrally arranged throughout the length of the caudal alae. Occasionally many are seen even beyond the latter. In some specimens it appears as if there are a few larger sessile papillae around the anal region, but this point has not been definitely ascertained. Caudal alae large and thick, meeting together in front of cloaca, 1·764 mm. long and 1·5 mm. in greatest width. Anus to posterior end 0·9 mm.

Female. Body 1·0 mm. in greatest diameter and 21·0 mm. long. Cuticle may be much inflated at posterior end. Collarette indistinct or very distinct, in some specimens even covering entire height of lips. Lips 0·075 mm. high and 0·144 mm. wide. Cephalic collarette about 0·23 mm. in diameter. Cervical papillae about 0·62 mm. and nerve-ring 0·47 mm. from anterior end of body. Excretory pore 0·7 mm. from anterior end of body, its duct leading vertically for a short distance and then bending obliquely forward. Oesophagus about 4·2 mm. long, its anterior muscular portion measuring 0·56 mm. long. Anterior portion narrower, 0·144 mm. in diameter at anterior end, and posterior portion at base 0·27 mm. in diameter. The vulva is very inconspicuous, but its position can readily be seen by a large ventro-lateral constriction of the body at about 6·0 mm. from the anterior end of the body. The genital pore can be seen in this concave area in lateral view as a somewhat raised region, the vagina leading obliquely backward. Uterus with two branches. Tail bluntly conical 0·72 mm. long. Eggs $48 \times 27\,\mu$, numerous, embryonated when deposited.

Discussion. The present specimens agree very well with those reported by Baylis except that they are larger, and are possibly provided with spicules. There is also an apparent difference in the number and arrangement of the caudal papillae. Baylis stated that "no trace of spicules has been found" while I can detect their presence in some of our specimens. I believe that there is a possibility that they may be present in all specimens, but since they are only slightly chitinized, it is rather difficult to see them. The number of caudal papillae is another structure which cannot be settled at the present moment. Baylis saw "four pairs of small and very inconspicuous post-anal papillae situated on the sides of a kind of ventral groove formed by folds of cuticle".

In our own specimens we have often seen a larger number of very inconspicuous papillae irregularly arranged throughout the length of the caudal alae. The discrepancy seems to be due to the minuteness of the papillae which has unquestionably made observation very difficult. Should there prove to be real differences in their number and arrangement between the two forms it may be necessary in the future to call the present specimens a distinct species.

The constriction of the area where the vulva is located, and the latter's position, appear to have a direct relationship with the form of the caudal extremity and the length of the body in the male. From Fig. 10, we note how the ventrally rolled tail of the male clasps the constricted area of the female. Moreover, we also see that the distance of the vulva from the anterior extremity is such that a male specimen can exercise two important functions, namely, those of copulating with the female, and feeding with the head end embedded in the stomach wall, at the same time, without depriving either worm of the power to move the body behind the head freely from one direction to another. Baylis has suggested that the constriction at the place where the vulva is found may be produced by the pressure of the caudal end of the male during copulation. But this seems not to be the case, since the depression is also present in all the immature forms.

Uncinaria longespiculum Maplestone, 1931
(Figs. 17–22)

A detailed description of both male and female specimens of this species as found in Canton is given below in order to elucidate certain structures which have not been treated in detail in the descriptions of previous workers.

Specific description. Body short, relatively stout, and generally straight, with a slight dorsal curvature at anterior extremity. In one lot, however, most specimens are bent ventrally. Cuticle thick and marked with minute striations from 3·5 to 4 μ apart. Head with six cephalic papillae and provided with subdorsal oral aperture, almost round in shape. Oral aperture guarded by a pair of chitinized plates. Oral capsule somewhat funnel-shaped and with several chitinized thickenings in its wall. From the dorsal aspect the lateral wall of the capsule is made up of three chitinized elements distinctly articulated. The first element slightly overlaps the second, which is at the level of the ventral teeth. The third element is the smallest, and may be absent in some specimens. Undoubtedly the annular thickening referred to by Baylis (1933) in *U. hamiltoni* is equivalent to the third piece when present. Dorsally and toward the median line there are two curved elements immediately behind the oral aperture. They form part of a chitinized structure connected anteriorly with the anterior margin of the first element and posteriorly with the region between the ventral teeth and the third element. From the lateral aspect the ventral wall is seen to be made up of two or three chitinized elements which correspond with the elements of the lateral walls. A transverse suture may

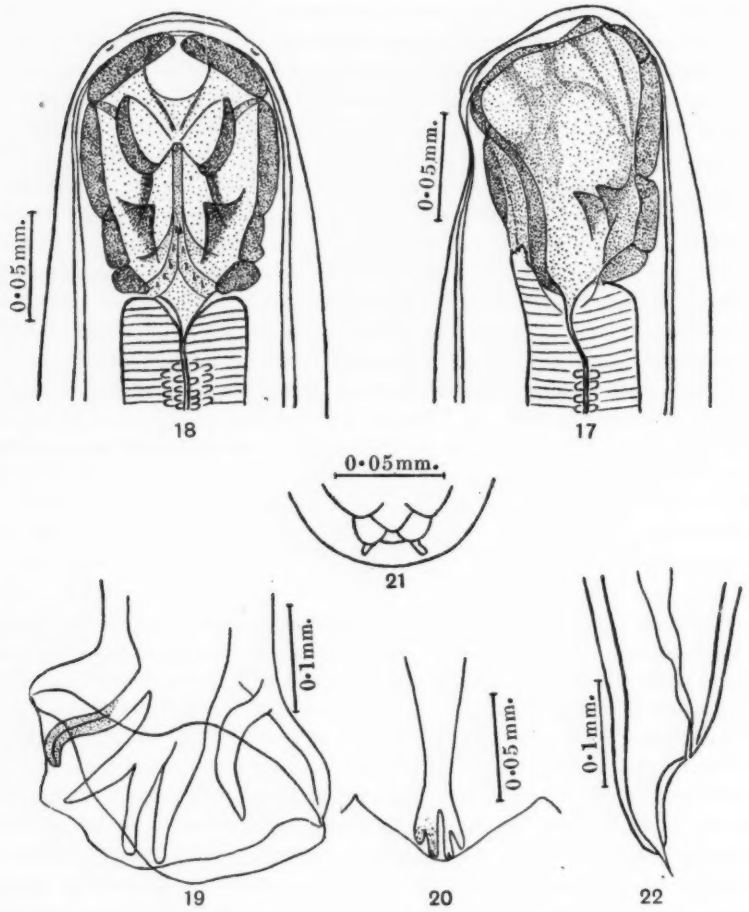


Fig. 17. *Uncinaria longespiculum*, lateral view of the anterior end of a male, showing the dorsal curvature and various chitinized elements.

Fig. 18. *U. longespiculum*, dorsal view of the anterior end of a male, showing the position of the oral aperture and various chitinized elements.

Fig. 19. *U. longespiculum*, lateral view of the bursa, showing the arrangement of the rays.

Fig. 20. *U. longespiculum*, dorsal ray of the bursa, showing unequal digitations.

Fig. 21. *U. longespiculum*, genital cone from ventral aspect. Note the two digitiform processes on the sides of the dorsal portion.

Fig. 22. *U. longespiculum*, lateral view of the tail of a female. Note the fine hair-like point.

sometimes be seen in the anterior third of the first element. The dorsal wall, from the lateral aspect, is made up of three chitinized elements, a short one immediately below the oral aperture and apparently equivalent to the median curved element seen in dorsal view, and behind it an inner longer element extending to the oesophagus, and an outer shorter one extending almost to the oesophagus. These two elements together represent the system of median curved elements. Two ventral teeth arise from near the base of the capsule. The oesophagus is enlarged at its posterior end. The dorsal oesophageal gland opens at the end of the dorsal gutter, which may be seen very distinctly in dorsal view, and as a more or less clear streak between the outer and inner chitinized elements in lateral view.

Male. Body 4·12–4·91 mm. long, with a maximal breadth of 0·288 mm. Buccal cavity 0·071 mm. in internal maximal breadth, and 0·117 mm. deep from base to anterior tip. Oesophagus 0·471 mm. long and 0·093 mm. in maximal breadth of terminal swelling. Nerve-ring 0·294 mm. from anterior end. Cervical papillae conspicuous, 0·376 mm. from anterior end. Excretory pore somewhat in front of cervical papillae. Spicules slender and equal or almost equal, transversely striated and finely pointed, 2·052 mm. long. Gubernaculum heavily chitinized, 0·1 mm. long. Pre-bursal papillae located somewhat subventrally, 0·214 mm. from posterior extremity.

Bursa with three lobes; dorsal lobe small and separated from lateral lobes by fairly deep indentations. Ventral rays cleft for about half their length. Lateral rays arise from a common trunk; the externo-lateral ray somewhat widely separated from the other laterals. Externo-dorsal rays arise from a common trunk with the dorsal ray. Dorsal ray bifurcated at its tip, and each branch gives rise to three unequal digitations. Genital cone consists of a ventral portion divided into a central conical element and two lateral processes, and a dorsal portion with two digitiform processes on its sides.

Female. Body 4·557–5·540 mm. long, with a maximal breadth of 0·353 mm. Buccal cavity 0·081 mm. in internal maximal breadth and 0·126 mm. long from base to anterior end of body. Oesophagus 0·511 mm. long and 0·114 mm. in greatest width at the posterior swelling. Nerve-ring 0·323 mm. and excretory pore 0·381 mm. from anterior extremity of body. Cervical papillae conspicuous, somewhat behind excretory pore. Vulva behind middle of body and 1·358 mm. from posterior extremity. A single subventral papilla present at level of vulva. Tail 0·094 mm. long, ending in a blunt tip surmounted by a fine hair-like point. A pair of minute lateral papillae present, approximately 0·038 mm. from posterior end of body. Eggs in the uterus have thin walls, measuring $68·3 \times 35 \mu$.

Discussion. The species was first described by Maplestone (1931) from a civet cat (*Viverricula malaccensis*) as *Uncinaria longespiculum*. A year later Chitwood (1932) described a species, *U. philippinensis*, from a Philippine civet (*Paradoxurus philippinensis*). The two species are very similar, and Baylis (1933), after comparing specimens from both sources, maintained that they

Table II. *Measurements of seven males in mm.*

	Minimum	Average	Maximum
Body size	4·6 × 0·252	4·52 × 0·2735	4·91 × 0·252
Cuticular striations	0·0035	Over 0·0035	0·004
Buccal cavity	0·07 wide 0·105 deep	0·071 wide 0·117 deep	0·073 wide 0·123 deep
Oesophagus	0·447 long 0·094 widest	0·471 0·093	0·482 0·108
Cervical papillae to anterior extremity	0·360	0·376	0·403
Excretory pore to anterior extremity	0·346	0·311	0·382
Nerve-ring	0·288	0·294	0·302
Spicules	1·837	2·052	2·205
Gubernaculum	0·095	0·101	0·108
Pre-bursal papillae to posterior extremity	0·108	0·214	0·237

Table III. *Measurements of seven females in mm.*

	Minimum	Average	Maximum
Body size	4·557 × 0·288	5·182 × 0·3343	5·54 × 0·353
Cuticular striations	0·0035	Over 0·0035	0·004
Buccal cavity	0·073 wide 0·115 long	0·081 0·126	0·084 0·133
Oesophagus	0·100 wide 0·475 long	0·114 0·511	0·112 0·526
Cervical papillae to anterior extremity	0·389	0·402	0·418
Excretory pore to anterior extremity	0·360	0·381	0·396
Nerve-ring to anterior extremity	0·295	0·323	0·338
Tail	0·081	0·093	0·101
Vulva to posterior extremity	1·102	1·358	1·47
Eggs		0·0683 × 0·035	

were identical and that the name *Uncinaria philippinensis* must fall into synonymy. Sandground (1933) described a new species of *Uncinaria*—and coincidently he also called it *U. longispicula*—from *Paguma larvata intrudens* from Tonkin. After comparing the descriptions of this species with those of Maplestone and Chitwood, and also with the present specimens, the present writer is convinced that *Uncinaria longispicula* Sandground is a synonym of *U. longespiculum* Maplestone.

Table IV is a summary of important characters of the specimens of Maplestone, Chitwood, Sandground and the author. It is to be noted from the table that there is a great deal of difference in the size of various parts. In the first place our present specimens are apparently the largest and consequently many other measurements are correspondingly greater. The most noteworthy difference of size is probably in the spicules. In the present specimens their length is 2·052 mm. and in those of Sandground 2·19 mm., in both cases the spicules being almost double the length of those of Maplestone's and Chitwood's specimens. It is also to be noted in this connexion that both our specimens and those of Sandground are from subspecies of *Paguma larvata*. A question may arise as to whether we would consider the length of spicules

as of specific importance. From the study of many specimens here, as can be noted from Table II, the writer has found that the spicules vary from 1·837 to 2·205 mm. in length, a range of 0·368 mm. It seems, therefore, quite possible that variations to the same extent or more would have been found in Maplestone's and Sandground's specimens if they had been more numerous. For this reason the writer feels that all belong to one species. Other differences of lesser significance are: the length of the tail in Maplestone's specimens; slight variations in the position of the vulva, and the size of the eggs.

Table IV. *Summary of measurements (in mm. unless otherwise stated) of specimens of Maplestone, Chitwood, Sandground and present author*

	U. longespiculum Maplestone	*U. philippinensis* Chitwood	*U. longispicula* Sandground	Present specimens
Body size	♂ 3·3 × 0·24 ♀ 4·0 × 0·36	3·29–3·38 × 0·18–0·20 3·3–3·50 × 0·25–0·30	3·62 × 0·29 4·55 × 0·45	4·52 × 0·274 5·18 × 0·334
Buccal capsule	—	♂ 0·08–0·095 × 0·06–0·08 ♀ 0·085–0·10 × 0·075–0·09	0·087 0·094	0·105–0·123 long 0·115–0·133 long
Oesophagus	♂ 0·42 ♀ —	0·42–0·44 0·46–0·50	0·40 0·48	0·471 0·511
Cervical papillae	— —	— —	— —	0·376 from ant. end 0·402 from ant. end
Excretory pore	— —	♂ 0·30–0·31 ♀ 0·34–0·36	0·29 0·32	0·311 from ant. end 0·381 from ant. end
Nerve-ring	— —	♂ 0·20–0·21 ♀ 0·26	0·29 0·32	0·294 from ant. end 0·323 from ant. end
Spicules	1·19	1·2–1·25	2·19	2·052
Gubernaculum	0·088	0·07–0·09	Gubernaculum (?) 0·025	0·101
Female tail	0·25	0·10–0·18	0·13	0·093
Caudal papillae	—	0·18 from post. end	—	0·214 from post. end
Vulva	1·7 from post. end	2·4–2·5 from ant. end	1·3 from post. end	1·358 from post. end
Eggs	60 × 32 μ	60–66 × 34–38 μ	55 × 32 μ	68·3 × 35 μ

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PARASITIC COPEPODS OF FISH FROM CEYLON. II

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(With 107 Figures in the Text)

In this second contribution to the study of parasitic copepods of fish from Ceylon eight species are described, four of which are new. The male of one species, namely that of *Euryphorus nordmanni* Milne-Edwards, is described for the first time. Of the three remaining species, *Caligodes laciniatus* Kröyer has only been recorded once (Heller, 1865) since it was originally described in 1863 and the comparison of *Caligus alalongae* Kröyer and *C. tenax* Heller makes it easier to identify the males of these two forms.

The type specimens of these new species, at present in the Department of Zoology, Ceylon University College, will in due course be lodged in the British Museum (Natural History).

(1) **Caligus alalongae** Kröyer (1863)

Host and record. Several males and females were taken from the gill chamber of *Caranx kalla* and two other *Caranx* spp. in April 1934.

Description of female (Fig. 1). Carapace rounded, equal to or less than half the entire length; frontal plates distinct, lunules prominent; eyes placed at about a fourth of the length of the carapace from its anterior end; median lobe larger than the lateral lobes and more than a third of the width of the carapace.

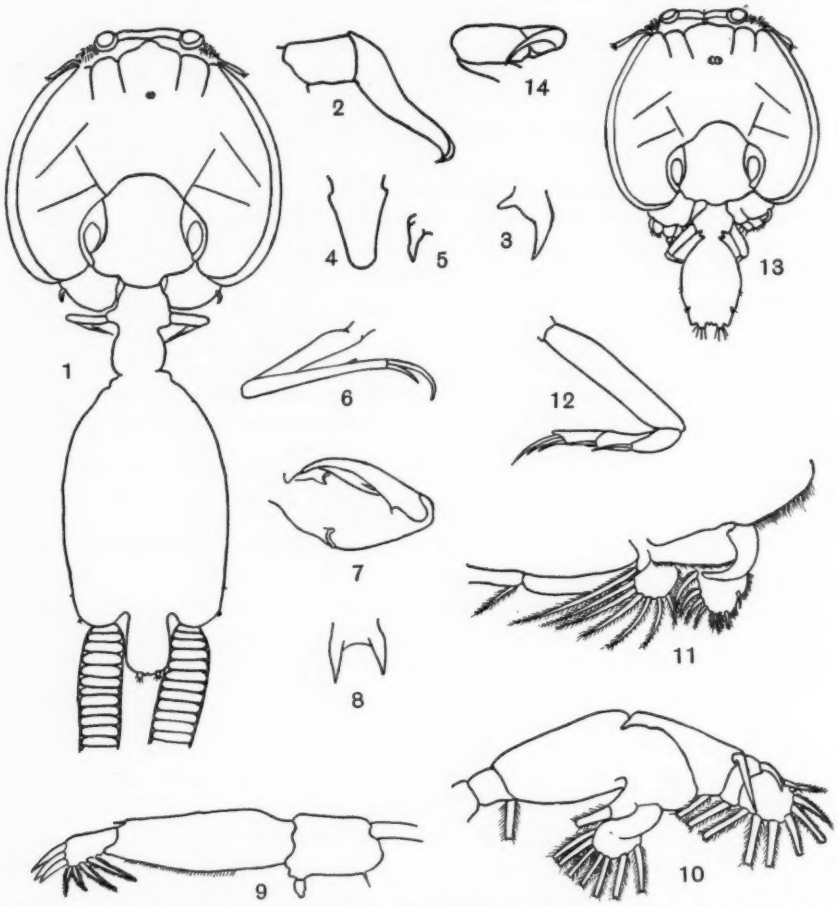
Free thoracic segment narrow, very much elongated and constricted behind the bases of the fourth legs, posterior half with convex lateral margins.

Genital segment about as long as the carapace and produced behind into distinct lateral lobes on either side of the abdomen.

Abdomen small, only about a third of the length of the genital segment, one-segmented; anal laminae minute with four small setae on each.

Second joint of the first antenna greatly elongated and provided with setae at the tip. Second antenna (Fig. 2) bears a long terminal claw. Maxillary hook (Fig. 3) has a swollen base carrying a short spur. Mouth cone (Fig. 4) elongated. First maxilla (Fig. 5) with a strong spine. Second maxilla (Fig. 6) slender, two-jointed, with two terminal spines and a third spine on the inner border of the second joint. Maxillipede (Fig. 7) with two small shelf-like projections on the inner side of the basal joint, terminal claw armed with a minute spine on its inner margin. Furca (Fig. 8) bears a pair of pointed prongs. First thoracic leg (Fig. 9) three-jointed, first joint bearing a seta and the rudiment of an endopodite, second joint long, furnished with a row of short, hair-like setae on its

posterior border and a small spine at its anterior distal end, third joint with three spines and four pinnate setae. Second leg (Fig. 10) biramous, the outer ramus with three joints, the first joint of the inner ramus well marked but the



Figs. 1–12. *Caligus alalongae* ♀. 1, entire animal, dorsal view; 2, second antenna; 3, maxillary hook; 4, mouth cone; 5, first maxilla; 6, second maxilla; 7, maxillipede; 8, furca; 9, first leg; 10, second leg; 11, third leg; 12, fourth leg.

Figs. 13, 14. *Caligus alalongae* ♂. 13, entire animal, dorsal view; 14, second antenna.

separation between the second and third joints not quite complete. Third leg (Fig. 11) has a strongly curved hook on the outer ramus. Fourth leg (Fig. 12) weak, four-jointed. Fifth leg represented by a minute spine, and sixth leg by a tuft of three similar spines on the postero-lateral corners of the genital segment.

Total length 4·5 mm.

Description of male (Fig. 13). Carapace more than half the entire length, otherwise as in the female.

Anterior portion of free thoracic segment similar to that of the female, posterior part, however, represented by a short region which bears a pair of small projections on the lateral margins.

Genital segment small, flask-shaped and separated by slight notches from the short one-segmented abdomen; anal laminae and setae as in the female.

Appendages like those of the female except the second antenna and the fifth leg. Second antenna (Fig. 14) with a proportionately longer basal joint and a shorter, sharply curved terminal claw; fifth leg with a tuft of three minute spines in addition to a single spine similar to that of the female.

Total length 2·3 mm.

(2) **Caligus tenax** Heller (1865)

Host and record. One female and four males were taken from the gill arches and the inner side of the gill cover of a *Caranx* sp. in May 1934.

Description of female (Fig. 15). Carapace a little wider than long, contracted in front, broader behind; frontal plates distinct, lunules prominent; eyes placed at about a third of the length of the carapace from its anterior end; lateral lobes of the carapace slightly overlap the corners of the median lobe.

Free thoracic segment short, narrowed anteriorly.

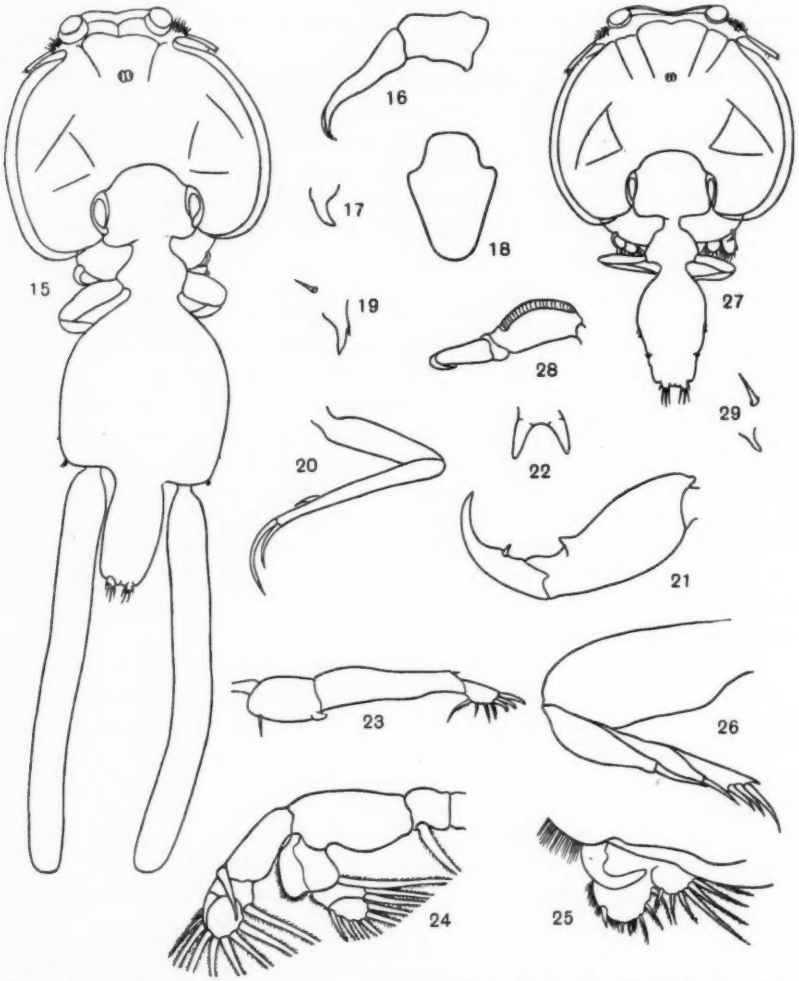
Genital segment acorn-shaped, two-thirds the size of the carapace.

Abdomen one-segmented, cylindrical, little more than half the length of the genital segment; anal laminae minute, each tipped with four setae of which the outer seta is smaller than the others.

First antenna with a short basal joint covered with setae and a very long terminal joint tipped with setae. Second antenna (Fig. 16) two-jointed, second joint forming an elongated claw. Maxillary hook (Fig. 17) with an enlarged base. Mouth cone (Fig. 18) stout. First maxilla (Fig. 19) consists of a strong spine carrying another minute spine at about the middle of its inner border and an accessory spine placed a little anterior to this. The two-jointed second maxilla (Fig. 20) with a small spine placed on the inner border of the second joint at about a third of its length from the tip and two terminal spines. Basal joint of the maxillipede (Fig. 21) with a small tubercle on its inner side nearer to the distal end, distal joint also with a spine on its inner border. Furca (Fig. 22) with two moderate, divergent, tapering prongs. First thoracic leg (Fig. 23) three-jointed, first joint with a pinnate seta and the rudiment of an endopodite on its posterior margin. Second leg (Fig. 24) biramous, rami three-jointed. Third leg (Fig. 25) also biramous, exopodite with a stout, curved claw. Fourth leg (Fig. 26) four-jointed, first joint stout and equal in length to the other three joints taken together. Fifth and sixth legs at the postero-lateral corners of the genital segment, fifth leg represented by a single minute spine, sixth leg by three small spines arising from a short stumpy base.

Total length 4·5 mm.

Description of male (Fig. 27). Carapace similar to that of the female but relatively larger.



Figs. 15–26. *Caligus tenax* ♀. 15, entire animal, dorsal view; 16, second antenna; 17, maxillary hook; 18, mouth cone; 19, first maxilla; 20, second maxilla; 21, maxillipede; 22, furca; 23, first leg; 24, second leg; 25, third leg; 26, fourth leg.
Figs. 27–29. *Caligus tenax* ♂. 27, entire animal, dorsal view; 28, second antenna; 29, first maxilla.

Free thoracic segment narrowed anteriorly to form a slender neck.

Genital segment barrel-shaped, separated behind from the abdomen by a slight notch on each side.

Abdomen indistinctly two-segmented, hinder segment the longer; anal laminae and setae as in the female.

Appendages, except second antenna, first maxilla and fifth leg, resembling those of the female. Second antenna (Fig. 28) with basal joint relatively longer, first maxilla (Fig. 29) without a minute spine on its inner border and fifth leg with three spines arising from a short base in addition to a minute spine.

Total length 3 mm.

Remarks. This species was established by Heller on a description of the female. Bassett-Smith (1898) claimed to have described the male, but his figure of it is so poor as to be unrecognizable and his description is lacking in detail. He figures and describes the maxillary hook as bearing a short spur. A basal spur on the maxillary hook is characteristic of *C. alalongae* Kröyer (=*C. carangis* Kröyer), but not of *C. tenax*. The males of these two species occurring on the same fish are not readily distinguishable and the specimen from which Bassett-Smith described the maxillary hook appears to have been a *C. alalongae* and not a *C. tenax*. Both sexes of the latter have been accurately figured and described by Wilson (1913).

(3) **Caligodes laciniatus** Kröyer (1863)

Host and record. The collection consists of two females taken from the Snake Gar *Strongylura* (*Strongylura*) *strongylura* (von Hasselt) in May 1934 and another lot of eight females from the Needle Fish *S.* (*S.*) *leiura* Bleeker taken in August 1934. In the former instance the parasites were found in the mouth on the lower jaw, their position of attachment being marked by a conspicuous haemorrhagic swelling within which the head and neck of the parasite were buried while the whitish body and light brown egg strings projected out from this swelling. The parasites from the Needle Fish were holding on superficially to the base of the tongue by means of the usual appendages.

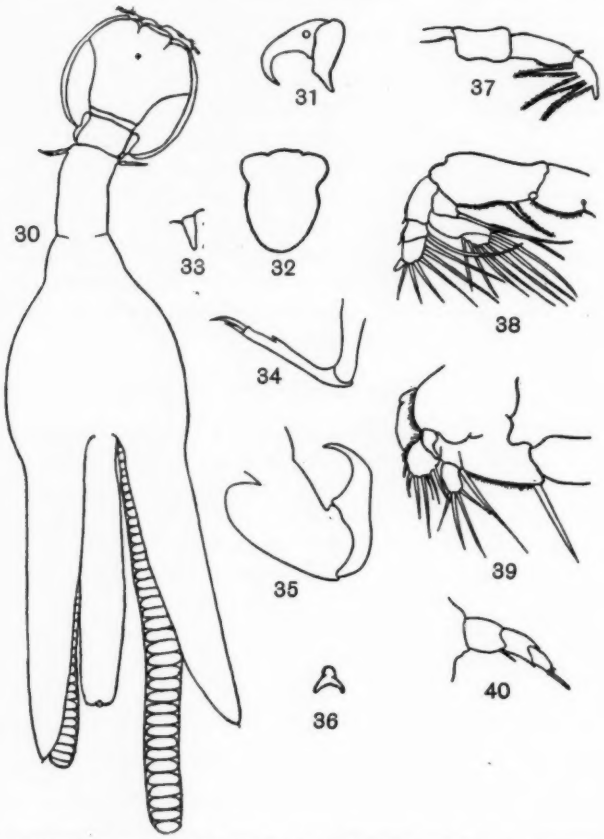
Description of female (Fig. 30). Carapace very small, oval in shape; frontal plates distinct, with a pair of minute, ventrally directed lunules; eyes at about a third of the length of the carapace from its anterior end.

Fourth thoracic segment about two-thirds the length of the carapace, clearly marked off from the third segment but passing behind almost imperceptibly into the genital segment.

Genital segment sac-like, narrow in front, becoming much swollen behind and produced at its posterior corners on either side of the abdomen into a pair of laminate processes tipped with a short spine. In some specimens from the Needle Fish these processes are filled with a milky-white substance and so have a rounded tapering form. They are as long as, or a little longer than, the cylindrical abdomen: anal laminae short, furnished with setae.

First antenna two-jointed: basal joint covered with short setae, terminal joint longer and club-shaped with setae at the tip. First joint of the second antenna (Fig. 31) short, with a basal spur; terminal claw fairly long. Maxillary

hook a small spine with a swollen base. Mouth cone (Fig. 32) stout. First maxilla (Fig. 33) a strong, blunt spine. Second maxilla (Fig. 34) with a cylindrical basal joint and a long, slender second joint tipped with two spines and also bearing a small spine on its anterior border. Maxillipede (Fig. 35) with a stout base and a strong terminal claw. Furca (Fig. 36) small, prongs short and



Figs. 30–40. *Caligodes luciniatus* ♀. 30, entire animal, dorsal view; 31, second antenna; 32, mouth cone; 33, first maxilla; 34, second maxilla; 35, maxillipede; 36, furca; 37, first leg; 38, second leg; 39, third leg; 40, fourth leg.

blunt and widely divergent. First thoracic leg (Fig. 37) uniramous, three-jointed: basal joint short, second joint longer with a short digitate process distally and its hinder surface with very short, hair-like setae along the distal two-thirds; the small terminal joint with a single spine at its tip and three pinnate setae along its posterior border. Second leg (Fig. 38) biramous, rami three-jointed: basal joint fringed with short, hair-like setae along its posterior

border, second joint longer, with a pinnate seta and a row of short setae along its posterior border, exopodite with a small spine at the ends of the first and second joints and a small digitate process along with six pinnate setae on its distal joint. Third leg (Fig. 39) also biramous, each ramus of two joints: second basal joint with a pinnate seta and a fringe of short setae along its posterior border; first joint of exopodite with a moderate hook, second joint with seven pinnate setae, both joints fringed with short setae on the outside; first joint of endopodite with a long pinnate seta at its distal end, terminal joint with four pinnate setae at its tip and a fringe of short setae on its outer side. Fourth leg (Fig. 40) uniramous, three-jointed and armed with a long spine at its tip.

Remarks. The specimens from the Snake Gar are distinctly smaller in size than those from the Needle Fish, the former being about 5 mm. in length while the latter average 7·5 mm. The dimensions (in mm.) of one of the latter specimens are as follows: Carapace 1·2; genital segment 2·5; free thorax segment 1; abdomen 3; entire length 7·7.

(4) **Lepeophtheirus spinifer** n.sp.

Host and record. Six females and three males were taken from the skin of a *Chorinemus* sp. in May 1934.

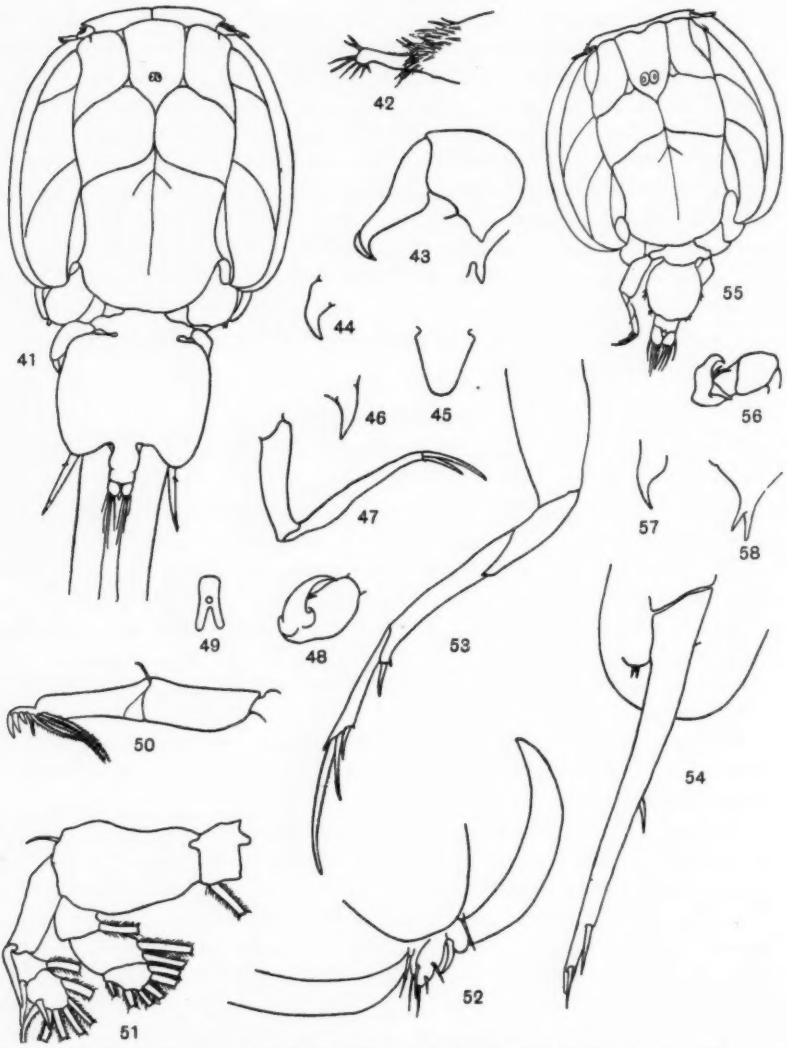
Description of female (Fig. 41). Carapace longer than broad, more than half the entire length; frontal plates distinct; posterior sinuses widely open; median lobe half the width of the carapace, projecting a little behind the level of the lateral lobes; eyes close to the anterior end.

Free thoracic segment very short, bases of the fourth legs projecting strongly outwards.

Genital segment wider than long, produced behind into prominent lobes on either side of the abdomen.

Abdomen small, half the length of the genital segment, two-segmented, second segment the shorter; anal laminae flattened, with four long setae and a minute seta on the inner side.

First antenna (Fig. 42) with setae on the basal joint and on the edge of the broad, flattened distal end of the terminal joint. Second antenna (Fig. 43) with an accessory spine at its base. Maxillary hook (Fig. 44) pointed. Mouth cone (Fig. 45) moderate in size. First maxilla (Fig. 46) a strong pointed spine. Second maxilla (Fig. 47) two-jointed, with two terminal spines, outer spine about two-thirds the length of the inner. Terminal claw of the maxillipede (Fig. 48) with a small spine on its inner border. Furca (Fig. 49) small, with two blunt prongs. First thoracic leg (Fig. 50) three-jointed: first and second joints of about the same length, first joint with a seta at its anterior end, third joint small with three terminal spines and four setae on its posterior border. Second leg (Fig. 51) biramous, rami three-jointed. Third leg (Fig. 52) also biramous but with two-jointed rami. Fourth leg (Fig. 53) uniramous, four-jointed: second joint tipped with a minute spine, third joint with a large spine and a minute spine to the outside of it, fourth joint with three spines subequal



Figs. 41–54. *Lepeophtheirus spinifer* ♀. 41, entire animal, dorsal view; 42, first antenna; 43, second antenna; 44, maxillary hook; 45, mouth cone; 46, first maxilla; 47, second maxilla; 48, maxillipede; 49, furca; 50, first leg; 51, second leg; 52, third leg; 53, fourth leg; 54, fifth leg.

Figs. 55–58. *Lepeophtheirus spinifer* ♂. 55, entire animal, dorsal view; 56, second antenna; 57, maxillary hook; 58, first maxilla.

in length. Fifth leg (Fig. 54) arising ventrally from posterior lobe of genital segment as a long, stout spine, extending backwards and outwards from its base considerably beyond the tip of the abdomen; with two very small setae lateral to the base and three small spines along its length.

Total length 4 mm.

Description of male (Fig. 55). Carapace similar to that of the female but relatively larger, about two-thirds of the entire length.

Genital segment small, oval in shape.

Abdomen of a single segment; anal laminae and setae as in the female.

Second antenna (Fig. 56) with a short basal joint and a strongly curved and branched terminal claw but without an accessory basal spine. First maxilla (Fig. 58) a two-pronged hook. Fifth and sixth legs visible on the sides of the genital segment, each consisting of three small spines arising from a short base. Other appendages as in the female.

Total length 2·5 mm.

(5) **Tuxophorus wilsoni** n.sp.

Host and record. A female and two males were taken from the skin of a *Chorinemus* sp. in May 1934.

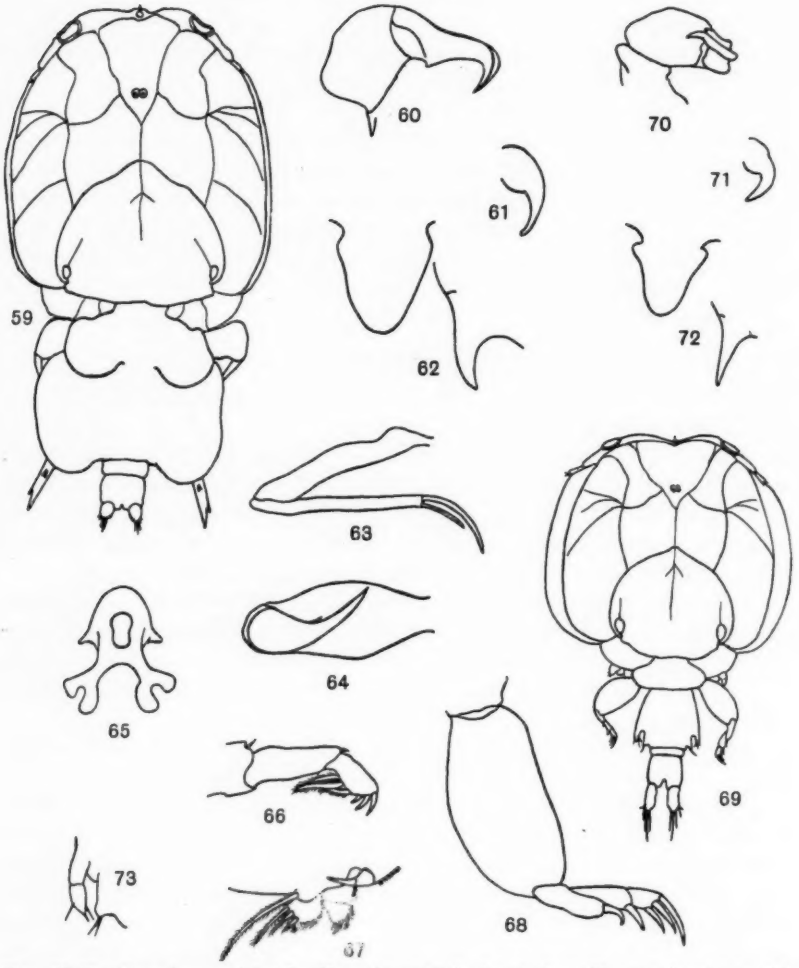
Description of female (Fig. 59). Carapace as long as broad, rounded in front, more than half the entire length; frontal plates distinct, lunules moderate but not projecting; posterior sinuses small; median lobe half the width of the carapace, projecting but little beyond the lateral lobes; eyes small, situate a third of the length of the carapace from its anterior margin.

Free thoracic segment short, about as wide as the median lobe of the carapace, with a pair of dorsal plates covering the bases of the fourth legs and overlapping the anterior corners of the genital segment.

Genital segment wider than long, produced into rounded lobes at the posterior corners.

Abdomen short, of two segments, second segment the longer; anal laminae oval in shape, each with three long terminal and two small lateral setae.

First antenna two-jointed: basal joint with short setae on its outer surface, terminal joint shorter, with setae at the tip. Second antenna (Fig. 60) with a short basal joint and accessory spine and a long terminal claw. Maxillary hook (Fig. 61) long and curved with a swollen base. First maxilla (Fig. 62) a large, slightly curved spine. Second maxilla (Fig. 63) of two joints of about the same length, the inner terminal spine nearly twice as long as the outer. Claw of the maxillipede (Fig. 64) with a small spine on its inner side at about the middle. Furca (Fig. 65) produced into two pointed processes on either side of its base; its branches bifurcate, secondary branches short, flattened and rounded at the ends. First and second joints of the first thoracic leg (Fig. 66) each with a spine at the distal anterior corner, third joint with three terminal claws and three long setae on its posterior margin. Rami of the third leg (Fig. 67) two-jointed. Fourth leg (Fig. 68) four-jointed: basal joint stout and longer than the three



Figs. 59–68. *Tuxophorus wilsoni* ♀. 59, entire animal, dorsal view; 60, second antenna; 61, maxillary hook; 62, mouth cone and first maxilla; 63, second maxilla; 64, maxillipede; 65, furca; 66, first leg; 67, third leg; 68, fourth leg.

Figs. 69–73. *Tuxophorus wilsoni* ♂. 69, entire animal, dorsal view; 70, second antenna; 71, maxillary hook; 72, mouth cone and first maxilla; 73, fifth and sixth legs.

remaining joints taken together, last three joints armed with five spines. Fifth leg arising ventrally from the postero-lateral lobes of the genital segment, extending as a strong spine backwards and outwards to the level of the tip of the abdomen; bifurcate distally, outer branch much smaller than the inner; with a small bifid spine on the dorsal surface behind the level of the lateral lobes. Sixth legs wanting.

Total length 4 mm.

Description of male (Fig. 69). Carapace similar to that of the female.

Free thoracic segment short, covered by a transversely elongated, oval dorsal plate, the latter overlapping the bases of the fourth legs and the anterior end of the genital segment.

Genital segment trapesoidal, fifth and sixth legs plainly visible in dorsal view on its postero-lateral regions.

Abdomen of two segments, shorter than the genital segment; first segment short, second much longer; anal laminae elongated, oval, almost as long as the second abdominal segment with setae like those of the female but decidedly longer.

Second antenna (Fig. 70) with a swollen basal joint and a second smaller joint terminating in a short claw. First maxilla (Fig. 72) a sharp elongated spine. Fifth leg a single conical joint furnished with three setae, and sixth leg represented immediately behind the latter by two setae arising from a lobe-like projection on the side of the segment (Fig. 73).

Total length 3 mm.

Remarks. This genus was created by Wilson (1908) to accommodate a single species *T. caligodes* Wilson. The addition of a second species agreeing with the first in its generic characters is therefore highly interesting. (This new species is named after C. B. Wilson, Esq., of the Department of Biology, State Normal School, Westfield, Massachusetts, in grateful appreciation of his extensive researches on the parasitic Copepoda.)

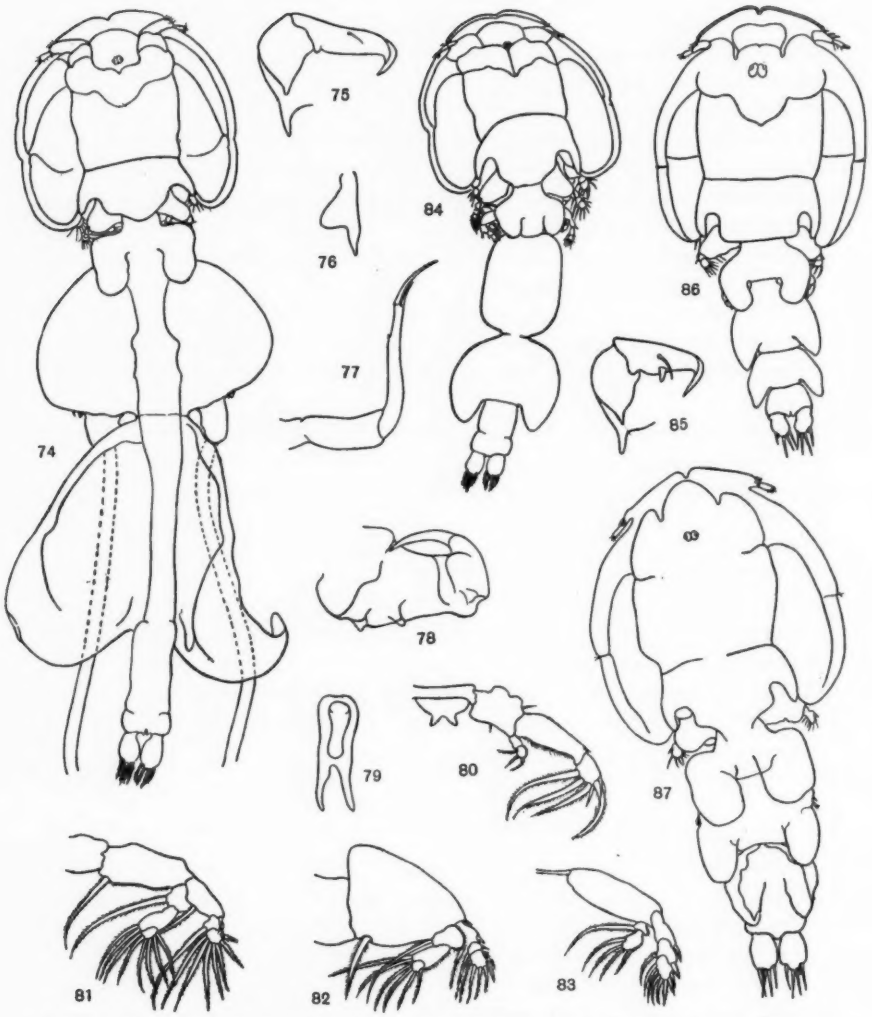
(6) **Euryphorus nordmanni** Milne-Edwards (1840)

Host and record. Several specimens of both sexes were obtained in September 1934 from the branchial chamber of the Dolphin *Coryphaena hippurus hippurus* and the lesser Dolphin *C. H. equisetis*. Two chalimus stages were also found on the skin of the latter.

Description of female (Fig. 74). Carapace small, as long as broad, equal to or less than a quarter of the total length (exclusive of the egg strings); frontal plates well developed; eyes placed well to the anterior end of the carapace; median lobe about half the width of the carapace; posterior sinuses shallow, widely open behind.

Free thoracic segment narrow; dorsal plates arising from the median third of its length and overlapping the anterior region of the genital segment.

Genital segment sac-like, in most specimens distended by the full oviducts



Figs. 74–83. *Euryphorus nordmanni* ♀. 74, entire animal, dorsal view; 75, second antenna; 76, first maxilla; 77, second maxilla; 78, maxillipede; 79, furca; 80, first leg; 81, second leg; 82, third leg; 83, fourth leg.

Figs. 84, 85. *Euryphorus nordmanni* ♂. 84, entire animal, dorsal view; 85, second antenna.

Figs. 86, 87. *Euryphorus nordmanni* ♀ chalimus stages.

and of a milky-white colour but in others oviduct not entirely filling up its half of the segment so that the outer portion of the segment appears as a thin, transparent membrane which curls over on to the dorsal side; with a pair of flattened lobes posteriorly, smaller than the dorsal plates and projecting backwards over the bases of the egg strings.

Abdomen nearly half the entire length, and composed of three segments; first segment longer than the other two taken together, its sides produced into wing-like extensions which reach to the extremity of the abdomen or even beyond, these extensions are usually laminate, in some instances, however, they are saccular towards the ends, while in others they are swollen in parts with a milky-white substance similar to that of the genital segment; second abdominal segment about half the length of the first; third segment the shortest; anal laminae flattened, with four pinnate setae and a small spine between the two outer setae.

Egg strings attain a length greater than that of the body.

First antenna two-jointed, basal joint armed with setae on its anterior face; second joint short, club-shaped, with a few setae at its tip and along the hind border. Second antenna (Fig. 75) also two-jointed, bearing a spur-like spine at its base, second joint forming a powerful hook with a small spine at about its middle on the inner side; an accessory spine present close to the base of this antenna. First maxilla (Fig. 76) a hook with a narrow base but swollen greatly in the middle. Second maxilla (Fig. 77) with a moderate basal joint and a longer but more slender second joint terminating in two spines, the outer spine twice as long as the inner; a small spine present on the anterior border of the second joint at about a third of its length from the tip. Basal joint of the maxillipede (Fig. 78) bearing a pair of tubercles between which the terminal claw can be held. Furca (Fig. 79) with a fairly broad, elongated base and two rounded, tapering prongs. An additional furca present between the bases of the first pair of thoracic legs (Fig. 80). All thoracic legs biramous. Rami of the first pair of legs two-jointed; outer ramus large, its first joint long and armed with a small spine anteriorly, posterior border furnished with fine hair-like setae, distal joint armed with three spines and four large pinnate setae; inner ramus small, its distal joint armed with three setae. Basal joint of the second leg (Fig. 81) with a large pinnate seta and a row of short, hair-like setae on its posterior border; rami of equal size, composed of three joints, each ramus bearing nine pinnate setae, the outer ramus in addition armed with three spines. Third leg (Fig. 82) with a stout, triangular basal joint bearing a pinnate seta posteriorly and a minute spine at its distal end; its rami being three-jointed. Basal joint of the fourth leg (Fig. 83) elongate-oval, its inner ramus of two joints, the outer of three. Fifth and sixth legs just visible in dorsal view at the corners of the genital segment to the outside of the posterior lobes; fifth leg represented by a single small spine arising from a short, stumpy base, sixth leg bearing three small spines on a similar base.

Total length 12 mm.

Description of male (Fig. 84). Carapace as in female, but nearly a third of the entire length.

Genital segment oval, without posterior lobes.

Abdominal segments retain the same proportions as in the female; first segment swollen and produced into lobes which project backward, these lobes not having the lamellar character of the corresponding extensions of this segment in the female; anal laminae as in the female.

Other appendages essentially similar to those of the female but second antenna (Fig. 85) possesses an additional spine on the inner side of its terminal joint and the fifth and sixth legs are lacking.

Total length 5·7 Mm.

Remarks. This species has only been recorded by Milne-Edwards (1840) who gives a brief description together with a dorsal view of the female. His specimen was taken from an unrecorded host in the "Eastern seas". This is, accordingly, the first description of the male and the only record of the host. Milne-Edwards was only able to make out two segments in the abdomen. This may have been due to the fact that in immature stages (Figs. 86, 87) the abdomen is only two segmented and also because the third segment is generally indistinctly marked even in the adult female. In the male, however, the three abdominal segments are clearly visible.

(7) **Lernanthropus cornutus** n.sp.

Host and record. Four females and a male were taken from the gills of the Needle Fish *Strongylura* (*Strongylura*) *leiura* Bleeker in November 1934.

Description of female (Figs. 88, 89). Cephalothorax longer than broad, a quarter of the total length and produced behind into a pair of stout, lateral horns projecting outwards at right angles to the long axis of the body; the sides of the cephalothorax extending ventrally to form flaps of considerable size.

Body covered by a dorsal plate divided into anterior and posterior regions by shallow marginal sinuses; anterior region narrow with convex sides and produced anteriorly to form a hump, posterior region wider and broadened out behind.

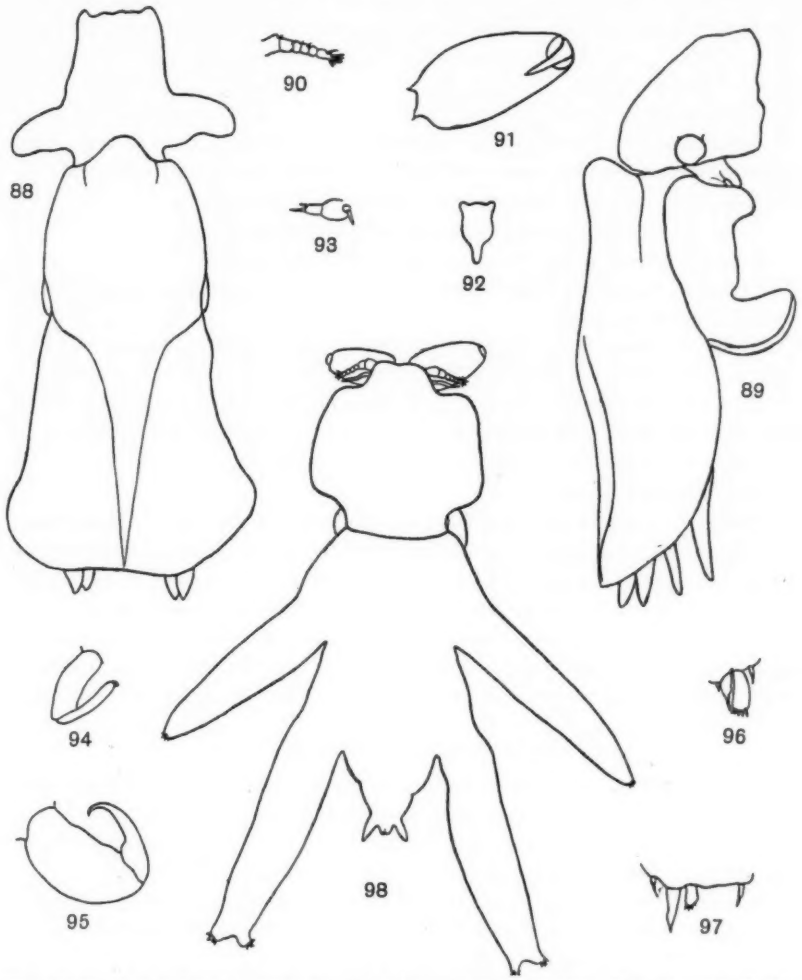
Genital segment short, with concave sides.

Abdomen a little longer but much narrower than the genital segment; anal laminae short, conical, tapering to a sharp point and extending to the centre of the posterior portion of the dorsal plate.

Egg strings more than twice as long as the body.

Antennae placed half-way along the groove of the cephalothorax formed by the lateral flaps: first antenna (Fig. 90) six-jointed, terminal joint setose; second antenna (Fig. 91) composed of a stout basal joint and a terminal claw. Mouth cone (Fig. 92) small and conical. First maxilla (Fig. 93) two-jointed: basal joint spherical with an accessory spine, terminal joint smaller, armed with two spines, the posterior being longer. Second maxilla (Fig. 94) with two

joints of much the same length, second joint slender and armed with a blunt claw at the tip. Maxillipede with a stout basal joint bearing a long terminal



Figs. 88–97. *Lernanthropus cornutus* ♀. 88, entire animal, dorsal view; 89, entire animal, side view; 90, first antenna; 91, second antenna; 92, mouth cone; 93, first maxilla; 94, second maxilla; 95, maxillipede; 96, first leg; 97, second leg.
Fig. 98. *Lernanthropus cornutus* ♂, entire animal, dorsal view.

claw (Fig. 95). Exopodite of the first thoracic leg (Fig. 96) armed with five short spines; endopodite conical, armed with a single spine reaching to the tip of the exopodite; two small spines arising from cylindrical bases on either side of this leg. Exopodite of the second leg (Fig. 97) shorter than the endopodite,

two spines on either side of this leg a little larger than those of the former. Third legs on a level with the marginal sinuses of the dorsal plate, folded in the usual manner and extending ventrally parallel to each other at right angles to the long axis of the body. Fourth legs biramous, divided almost to the base, rami flattened, acuminate, projecting but little beyond the posterior margin of the dorsal plate.

Total length 5 mm.

Description of male (Fig. 98). Cephalothorax about as wide as long, with more or less parallel sides, narrowed behind to form a neck connecting with the third segment and with an antennal area marked off in front.

Third and fourth segments as broad as the cephalothorax.

Genital segment short, narrower than the fourth segment.

Abdomen conical, a little longer than the genital segment; anal laminae short, rounded, tapering.

Third legs long, rounded processes extending diagonally backwards and tapering towards the extremities, the latter armed with a circlet of five or six short spines. Fourth legs a little longer, stouter, cylindrical and dividing at the ends into two short stumps their tips armed with a circlet of short spines as in the preceding legs. Other appendages as in the female.

Total length 2·5 mm.

Remarks. Both in its specific characters and its size this form is intermediate between *L. tylosuri* Richiardi (1880) the female of which is 7 mm. in length and *L. chlamydotus* Wilson (1922) the female of which is only 3 mm. It resembles the former and differs from the latter in the presence of a pair of lateral horns to the cephalothorax. It resembles the latter in the general appearance of the body region of both sexes but the cephalothorax, antennae, maxillae and first and second thoracic legs are markedly different.

(8) **Lernanthropus pristipomoidis** n.sp.

Host and record. A female and a male taken from the gills of *Pristipomoides typus* Bleeker in July 1934 are made the types of this new species.

Description of female (Fig. 99). Cephalothorax with an antennary region marked off in front and sides produced ventrally to form thin flaps.

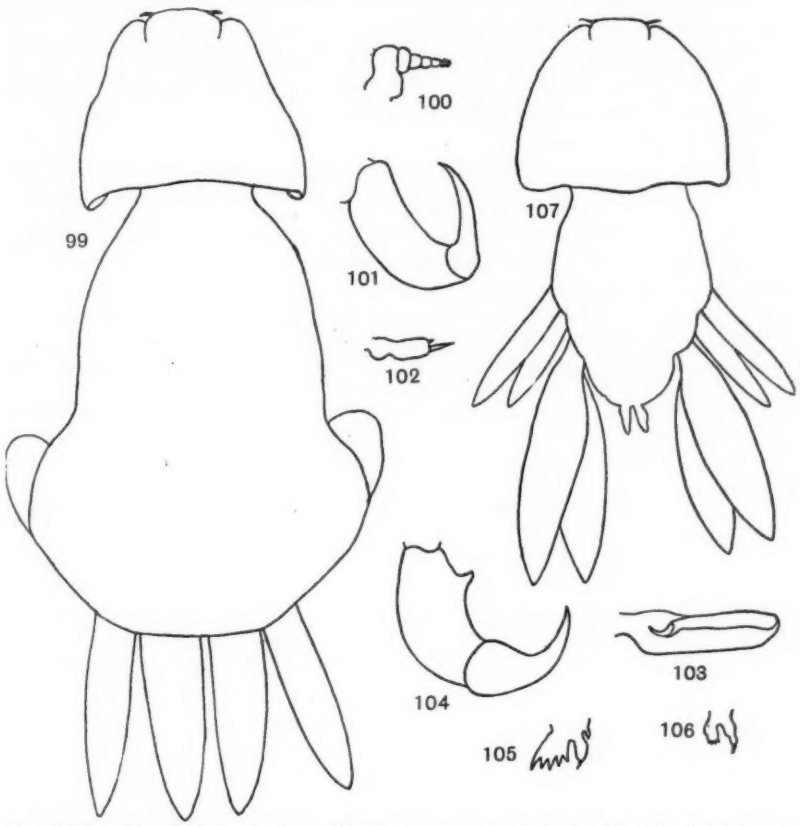
Dorsal plate of a single piece, divided into anterior and posterior regions by shallow marginal sinuses at the level of the third legs; anterior region narrowed in front, posterior region shorter and wider.

Genital segment short, with convex sides.

Abdomen shorter than the genital segment; anal laminae small, triangular and extending to within a short distance of the posterior border of the dorsal plate.

First antenna (Fig. 100) six-jointed; first joint large and stout, the remaining joints directed backwards at a right angle to it, terminal joint setose. Second antenna (Fig. 101) consisting of a stout basal joint with a strong terminal claw. Mouth cone short, conical. First maxilla (Fig. 102) indistinctly

two-jointed; first joint spherical, second joint longer, oval, and armed at the tip with two spines the posterior of which being larger. Second maxilla (Fig. 103) two-jointed; basal joint cylindrical and the slender terminal joint ending in a claw. Maxillipede (Fig. 104) with a moderate basal joint and a long claw.



Figs. 99–106. *Lernanthropus pristipomoidis* ♀. 99, entire animal, dorsal view; 100, first antenna; 101, second antenna; 102, first maxilla; 103, second maxilla; 104, maxillipede; 105, first leg; 106, second leg.

Fig. 107. *Lernanthropus pristipomoidis* ♂, entire animal, dorsal view.

Exopodite of the first thoracic leg (Fig. 105) with five spines, the oval endopodite with only a single spine; a minute spine placed internal to the endopodite. Exopodite of the second leg (Fig. 106) armed with four small spines, endopodite longer and armed with a single spine. Third legs folded in the usual manner, projecting downwards perpendicularly. Fourth legs divided to within a short distance of the base, rami broad, flattened and acuminate.

Total length 4 mm.

Description of male (Fig. 107). Cephalothorax as in the female but ventral flaps scarcely developed.

Thoracic region widest at the third segment. Fourth segment narrower than the third.

Genital segment short and indistinctly marked off from the abdomen; anal laminae twice as long as broad.

Third legs biramous divided almost to the base; rami flattened, acuminate, about half as long and half as broad as the rami of the fourth legs. Other appendages similar to those of the female.

Total length 2·5 mm.

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ON THE GENUS *CYBICOLA* BASSETT-SMITH (1898)

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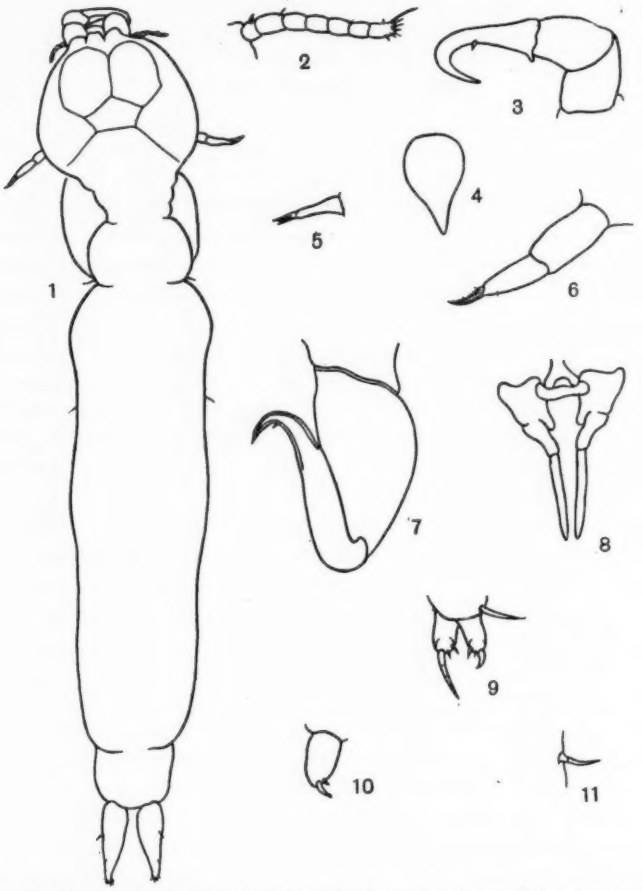
(With 11 Figures in the Text)

Bassett-Smith (1898 *a*) described a new parasitic copepod from the gills of *Cybium guttatum* at Bombay and named it *Helleria armata*, but later (1898 *b*) altered the name of the genus to *Cybicola* as the former name happened to be preoccupied. This parasite was not again recorded until the present author (1935) redescribed the female from the gills of *Scomberemorus commersoni* (Lacepede) (=*Cybium commersoni*) and at the same time suggested the transference of this species to the genus *Pseudocycnus* Heller (1865). The reasons for this suggestion were based on a comparison of the female of Bassett-Smith's species with the females of the two known species of *Pseudocycnus* (*vide* Wilson, 1922). Now, however, the author has been able to obtain from the same host a male of this copepod which is here described. The evidence from this description concludes the argument in favour of the inclusion of this form within the genus *Pseudocycnus*.

Description. General shape (Fig. 1) elongate. Head more or less rounded, fused with the first thoracic segment to form the cephalothorax which is narrowed posteriorly. First antennae directed laterally; second antennae projecting anteriorly. Second maxillae visible outside the lateral margins of the cephalothorax and maxillipedes appearing as large lateral lobes below the posterior region of the cephalothorax and the second thoracic segment. Latter incompletely fused with the first and third thoracic segments and about two-thirds as wide as the head. Third segment nearly as wide as the head, fused with the fourth and succeeding body segments to form the elongated, cylindrical trunk region. Abdomen one-segmented, narrower than the genital segment: anal laminae foliate, a little longer than the abdomen.

First antennae (Fig. 2) seven-segmented, terminal segment setose. Second antennae (Fig. 3) three-segmented, forming strong prehensile organs; terminal claw strongly curved and sharply pointed with a small spine on its inner margin. Mouth-tube (Fig. 4) pear-shaped. First maxillae (Fig. 5) two-segmented, basal segment long, terminal segment much shorter, bifid at the tip. Second maxillae (Fig. 6) two-segmented, first segment cylindrical, second segment longer and ending in a claw the concavity of which is covered with numerous minute setae. Maxillipedes (Fig. 7) large, two-segmented, second segment ending in a strong, curved claw which carries a minute spine on its inner border. Appendages of the first thoracic segment modified to form a pair of

elongated styles (Fig. 8) arising from flattened bases. Second thoracic appendages form biramous swimming legs (Fig. 9) consisting of a basal segment and one-segmented rami; basal segment with a large seta on its outer margin; rami of about equal size, endopodite tipped with a long jointed seta and two smaller setae, exopodite with three setae the outermost of which is the largest.



Figs. 1–11. *Pseudocycnus armatus* ♂. 1, entire animal, dorsal view; 2, first antenna; 3, second antenna; 4, mouth tube; 5, first maxilla; 6, second maxilla; 7, maxillipede; 8, first thoracic legs; 9, second thoracic leg; 10, third thoracic leg; 11, fourth thoracic leg.

Appendages of the third thoracic segment (Fig. 10) uniramous, one-segmented swimming legs tipped with two or three setae, the outer seta larger than the others. Fourth legs represented by a seta arising from a short, stumpy base on the lateral margins of the segment (Fig. 11).

Colour whitish.

Dimensions (in mm.). Cephalothorax 0·6; thorax and trunk 1·6; abdomen and anal laminae 0·4; total length 2·6.

Discussion. The genus *Cybicola* was defined by Bassett-Smith (1899) as follows: "Head rounded. Thorax with three distinct segments bearing lateral lobes but no dorsal plates. Genital segment very long. Abdomen small, with two lanciform appendages. Anterior antennae six-jointed. Posterior antennae three-jointed, strongly hooked at the end. Second maxillipede very large, basal joint robust. Three pairs of thoracic limbs, all rudimentary, the first biramose, the second uniramose, the third stump-like.

Male smaller. Posterior antennae strongly prehensile; no thoracic lateral lobes."

Bassett-Smith also remarked (1898 *a*) that this genus "is most nearly related to *Pseudocycnus* Heller but having these generic differences: (1) many jointed anterior antennae, (2) three-segmented thorax bearing only three pairs of limbs and (3) enormously enlarged maxillipedes".

Of these characters (1) and (3) are obviously not of a generic nature. *P. appendiculatus* has four-segmented anterior antennae and *P. buccatus* six-segmented anterior antennae and the maxillipedes are quite large also in these two species. With regard to the number of thoracic segments, it is even more evident in the male than in the female that four segments are present. The first segment which is fused with the head possesses a distinct pair of appendages. Though Bassett-Smith described this pair of appendages he made no attempt to associate it with any segment and hence he identified only three segments which are in fact the second, third and fourth thoracic segments. Moreover, it is seen from a comparison of this male with the male of *P. appendiculatus* that, but for the lateral extensions of the fourth segment of the latter, they resemble each other very closely—a resemblance which is further strengthened by the similarity of their appendages, except perhaps the first thoracic pair. These differences are not sufficient to justify the separation of the two species into different genera and therefore the genus *Cybicola* Bassett-Smith becomes a synonym of *Pseudocycnus* Heller and *Cybicola armata* Bassett-Smith synonymous with *Pseudocycnus armatus* (Bassett-Smith).

In conclusion the genus *Pseudocycnus* may now be defined as follows:

Female. Head fused with first thoracic segment, second and third segments free; fourth and fifth segments fused with the genital segment into a cylindrical body several times longer than wide, and of about uniform diameter throughout its length. Abdomen one-segmented, narrower than the genital segment. Egg strings filiform, longer than the body, eggs minute, numerous and strongly flattened.

First antennae of several segments, with a tuft of setae at the tip; second antennae prehensile, armed with a strong claw. Mouth tube short. Second maxillae uncinate, setiferous; maxillipedes large, with a terminal claw. First thoracic legs reduced to single laminae or altogether absent; second legs

biramous, rami one-segmented, setiferous; third and fourth legs uniramous, one-segmented, with terminal setae.

Male. Head fused with the first thoracic segment, latter forming a short neck between the head and second thoracic segment. Second thoracic segment free or only partially free. Third, fourth and fifth segments fused with the genital segment to form the trunk. Abdomen one-segmented, anal laminae foliate.

Second antennae and maxillipedes comparatively larger than in the female. First thoracic legs biramous, rami one-segmented, or they may be modified to form a pair of "styles". Remaining appendages very much as in the female.

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A COCCIDIAN FROM THE EGGS OF *THALASSEMA NEPTUNI* GAERTNER

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(With Plates XX–XXII, containing Figs. 1–32, and Figs. I–IV in the Text[1])

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I. Introduction

In 1881 Ray Lankester published some notes on the anatomy of the echiurid worm *Thalassema neptuni* Gaertner collected by him on the south coast of Devon in the month of March. Since the breeding season of this worm comes later in the year, only one of the hundred he examined was a mature female containing eggs in the distended genital pouches (nephridial sacs). But the observant naturalist noticed that the contents of these pouches were not normal, and he recorded that the eggs were "in a state of decomposition and infested (to the number of about one in five) by a *Gregarina*".

In the ninth edition of the *Encyclopaedia Britannica*, Lankester (1885), writing the article on Protozoa, makes casual reference to "*Monocystis thalassemae*" and gives a picture of its "chlamydospore".

Minchin (1903) mentions *Monocystis thalassemae* in a list of Sporozoa found in worms. The Goodrichs (1921), when working on *Gonospora minchinii*, a gregarine occurring in the egg of *Arenicola*, naturally followed up reference by other authors to Sporozoa in similar situations. Lankester showed them

[1] Figures occurring in Plates are indicated by Arabic, and text-figures by Roman, numerals.

some sketches he had made when studying *Thalassema*, and they saw at once that this "gregarine" was something very different from the organism with which they were concerned.

In September 1929, while one of us (H. N. R.) was working at Plymouth, Prof. A. D. Hobson spoke to him of the infection of *Thalassema* eggs by some protozoan parasite—an infection at times so heavy as to hamper seriously the fertilization study he was making. We soon found that the parasite was Lankester's "gregarine" of 50 years before: but we also saw that it had been classified wrongly, for we had the sexual forms in sufficient abundance to convince us that the course of gamete formation and sporogony was typically coccidian. Coccidia have been recorded from the male gonad of various animals; but, so far as we know, this is the first record of such a parasite in the female germ cells.

II. Materials and methods

Since eight of the twelve mature females we examined in 1929 were in some degree infected, we did not anticipate any trouble in obtaining an adequate supply of the coccidian in the following year. But the breeding season of the worm proved of more uncertain date than we had been led to expect: and we have also found that the incidence of infection is very variable. We paid three further visits to Plymouth in August and September (1930, 1931, 1932), and we had living material sent to us in London from time to time: but the net result of our examinations was that out of 935 worms only twenty-five were mature females showing any noticeable degree of infection. Even where the infection was heavy, it was usual to find the eggs in all four genital pouches containing parasites at much the same stage of development; and, while the sexual phase was common enough, we met with schizogony on only three occasions.

When the female is mature, the four genital pouches extend nearly half the length of the body and are filled with the ripening eggs, which float in the blood that enters from the coelom: as the muscular walls of the pouch contract rhythmically, the contained eggs are driven to and fro. The egg-filled pouch has an orange tinge: but if the contents are heavily infected with coccidia, it appears speckled with greyish white.

We usually removed one pouch and examined it under the slight pressure of a cover-slip. If parasites were present, we then made hanging-drop preparations and fixed smears of those eggs that had escaped on to the slide; the rest of the material was fixed and embedded for section cutting. The three other pouches were more cursorily examined and then fixed. Prolonged observation of the living organism gave us little information, for it is opaque and immobile. We constantly examined samples of blood from the coelom, in the hope of finding parasites travelling to the eggs; and we searched vainly through many sections of the gut for intracellular stages there.

We found that the best fixative for smears and for whole nephridial sacs

was Duboscq and Brasil's modification of Bouin's fluid: we have also employed Schaudinn's fluid, Flemming's fluid (with and without acetic acid) and Helly's fluid. Material fixed in Helly's fluid was treated after sectioning with Altmann's stain: but we mainly relied on Delafield and on Heidenhain's haematoxylin, counterstained with chromotrop 2R. Delafield proved especially useful: male and female parasites tend to take on different tints, and, for some reason, the characteristic granules in the cytoplasm survive this treatment better than they do others. In the Helly-fixed and Altmann-stained material, the granules appear still more nearly as they do in the living organism, but the nuclear pictures are not so good.

We cut sections varying in thickness from 4 to 15μ: on the whole, the thicker sections were the more helpful.

III. DESCRIPTION OF THE PARASITE

It seems simplest to prelude our description with the statement that this is a polysporocystid eimeriid coccidian—belonging, that is, to the same group as do Aggregata and Merocystis, but distinguished from these genera by its large vermiform trophozoites and by the fact that schizogony and sporogony occur in the same host, and in the same organ thereof.

(i) *Schizogony*

We have found the schizogonic phase on only three occasions, and always in worms that were without vermiform parasites or maturing sexual forms. The material was extremely sparse, and the few schizonts present were not only full grown but in advanced stages of division. With one exception, they lay in vacuoles within degenerating eggs: in this worm, where only four schizonts were present, one was embedded in the wall of the egg-sac.

At this stage, the schizonts are deeply lobed, subspherical masses, measuring from 50 to 80μ in diameter. The merozoites develop immediately below the pellicle, and their formation is preceded by formation of numerous nuclei at the periphery. Fig. 1 shows the surface view of part of a fairly advanced schizont in which some of the nuclei are still dividing. We have not been able to count the chromosomes with certainty, but their number does not exceed seven.

Fig. 2 shows a section through a schizont covered thickly with transparent, sausage-shaped merozoites.[1] Each merozoite measures about 10μ in length. The nucleus lies near the middle of the body and stains very densely: it seems to consist of a thick-meshed chromatin network (Fig. 3). Behind it there is sometimes a vacuole in the cytoplasm: we observed no differentiation anterior to the nucleus.

[1] We wish to correct an error in our preliminary note (1929). We stated that the schizont liberates about fifty merozoites. What we mistook for schizogony then were groups of developing sporoblasts: we were misled by the extreme tenuity, or even complete absence, of the oocystic envelope in this coccidian.

(ii) *Development of the sexual forms*

A single schizont produces such a large number of merozoites that only two or three asexual parasites within one genital pouch would be quite sufficient to account for the heavy infection with the sexual forms that we have commonly observed.

Presumably the merozoites escape from the worm's egg in which they were developed and invade others in their neighbourhood. (Where the infestation with sexual parasites is very heavy, the wall of the sac may also be attacked: sexual parasites developing in this abnormal situation are usually undersized and often degenerate.) The smallest parasites that we have found within an egg measure about $19 \times 5\mu$ (Fig. 4): the nucleus lies midway in the body and contains a dense, centrally placed karyosome and chromatin granules scattered on a reticulum. Growth in length is much more rapid than in width (Fig. 5); and eventually a worm-like form is assumed, the body lying curved within the host egg, the diameter of which it greatly exceeds.

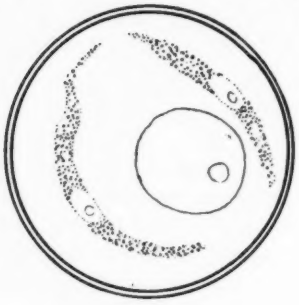

Fig. I.

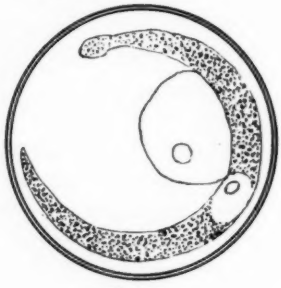

Fig. II.

Fig. I. Two young parasites within the egg of *Thalassema*. ×300 approx.
Fig. II. Large vermiform parasite. ×300 approx.
(Free-hand drawings by transmitted light. The parasitized egg is diagrammatically represented.)

In life these trophozoites look like greyish streaks within the egg, when seen by transmitted light (Fig. I): by reflected light they appear a glistening white. Their cytoplasm is crammed with coarse, irregular granules, the chemical nature of which we have not determined. As growth proceeds, one end of the body tends to become spatulate, while the other is tapering (Figs. II and 6). The parasites never move within the egg, and when artificially released they remain quite immobile. The thin pellicle shows no differentiation of any kind, and the contained granules are stationary.

As growth proceeds, the appearance of the nucleus changes. The karyosome becomes large and may show some complexity of structure: the chromatin lying between it and the nuclear membrane appears as a cloud of fine, more faintly staining dust (Fig. 5).

By the time the parasites are full grown, the egg shows clear signs of degeneration: but its contents are usually not completely used up until the spores have been formed; by then they have usually also been invaded by the worm's blood corpuscles.

The mature vermiform individuals proceed now to shorten and thicken (Fig. III), and as they do so their cytoplasm becomes so dense that it is impossible to detect the nucleus in the living state. By the time they are spherical they look almost black by transmitted light (Fig. IV). The largest sphere that we measured was 75μ: usually they are a good deal smaller than that, and one concludes that the great reduction in volume is caused by escape of fluid through the elastic and shrinking pellicle.

Fig. III.

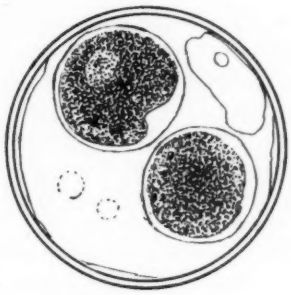

Fig. IV.

Fig. III. Vermiform parasites shortening and thickening in preparation for the sexual phase. ×300 approx.

Fig. IV. Condensed, subspherical gametocytes. ×300 approx.

(Free-hand drawings by transmitted light. The parasitized egg is diagrammatically represented.)

In recent years a good deal has been written concerning the changes that take place in the nucleus of coccidia prior to gamete formation. We are unable to supply details for the *Thalassema* parasite. Broadly, what happens is that, as the organism shortens and thickens, the nucleus assumes an ovate form, with its long axis at right angles to that of the body; and the karyosome shows increasing complexity, ultimately exuding siderophilous material in granules into the nucleoplasm. Sometimes, as in Fig. 14, there appears to be a micropyle in the vacuolated outer zone of the karyosome, and through this the dark-staining material emerges. None of these granules show any reticular structure, and we have been unable to trace their fate. Some of them and the outer shell of the emptied karyosome may persist in the female until after fertilization: after that, all trace disappears.

(iii) *Microgametogenesis*

We are unable to distinguish between male and female parasites while they are in the vermiform condition. We have noticed that some have a much less granular cytoplasm than others of comparable size; and, as the indubitable

males at the spherical stage show relatively few granules and have a finer-meshed cytoplasm than females alongside them in the same preparations, the state of the cytoplasmic content may be some index to sex even before the rounding-off process begins.

Undoubtedly there must be a size difference also, for, on the average, the spherical male gametocyte is considerably smaller than the female. Fig. 7 shows an extreme case of this. The smallest male we measured was 23 μ in diameter, and we once found one with a diameter of 65 μ; the average, however, is 30 μ. The size attained probably depends a good deal on the degree of crowding and the consequent amount of food available: it is common to find at least two parasites within an egg, and sometimes, as shown in Fig. 10, there may be as many as four.

As in that picture, the gametocytes within one egg may all be of one sex; but commonly both sexes are represented (Figs. 7, 8, 9). The cytoplasm of the male in process of gamete formation tends to stain more darkly than that of the female, and, as noted above, it contains fewer of the characteristic granules. It is mainly on such characters that one must depend for distinguishing a male with dividing nuclei from a zygote at the corresponding stage.

Fig. 16 shows a male in which the nucleus is preparing for the first division. The nucleus has moved to the periphery, and a group of chromosomes is assembled at one pole: the nuclear membrane is fading, one of the chromosomes extends beyond it, and the ejected karyosomic material lies in the cytoplasm. In Fig. 17 several nuclei have been formed, and one anaphase pole is shown. Wherever they can be counted, the number of chromosomes is seven. The count here is less difficult than in *Merocystis kathae*, where Patten (1935) states that the chromosomes are constantly bent into V or J shapes at anaphase: in the *Thalassema* coccidian, while such bending does sometimes occur (as in the prophase shown in Fig. 23), there are usually not more than seven ends present at the anaphase pole. The seventh chromosome, however, is very small, and is often hidden by the others. There are no centrosomes at this stage.

In Fig. 8 a small male is depicted in which the peripheral mitotic figures are more numerous, and in Figs. 9 *m* and 10 *a* the ultimate nuclei of the gametes are shown, each contained in a hummock of cytoplasm: over the whole lies the loosened pellicle, beneath which the gametes are formed. A small portion of the periphery is shown in Fig. 19, with two compact nuclei and one anaphase pole of a final mitotic figure: at this stage a centrosome appears for the first time, and survives as a basal granule from which a rhizoplast runs to the point of emergence of the flagella (Fig. 20).

After they have condensed, the nuclei then elongate, carrying the surface cytoplasm with them, until the whole sphere is covered with slender processes, from the distal ends of which sprout two flagella (Fig. 10 *b* and *c*). When it is about 12 μ in length the microgamete of our coccidian bears a strong resemblance to that of *Aggregata eberthi*, for an undulating membrane runs along one side of the body. The gametes stain very densely throughout, and in few could we

distinguish nucleus from cytoplasm: Fig. 21 shows the appearance presented at this stage in an unusually well differentiated specimen. A minute vacuole may lie close to the nucleus and about one-third of the way from the flagellar end: the occurrence of this vacuole is not invariable, but it appears so often in our preparations that we do not consider it to be an artefact. Elongation continues, and when the gamete breaks away from the central residuum it is a slender thread, tapering at both ends, and staining homogeneously: its length is about 20μ.

Male and female parasites lying within the same egg are seldom mature at the same time: generally the microgametes have to penetrate other eggs in order to effect fertilization. Their entrance is doubtless facilitated by some break-up of the membrane surrounding the parasitized egg, which, by this time, is often invaded by corpuscles from the worm's coelom.

(iv) *The female parasite*

Extreme measurements of rounded-off macrogametocytes are 40 and 75μ: the average diameter is 50μ. The cytoplasm tends to stain much more faintly than in the male and takes a pinker tinge with Delafield: it is more coarsely vacuolate, and the glistening granules characteristic of the vermiform stage are more abundant. The nucleus is at first approximately central in position (Figs. 7 and 8): it shows a faintly staining network and the degenerate remains of the karyosome.

We have not observed fertilization, although we have sometimes seen the cone of reception. We incline to think that the spindle shape acquired by the nucleus here, as in other coccidia, is a post-fertilization phenomenon (Fig. 9*M*); but since an oocystic membrane is seldom formed by our parasite, we have not this useful criterion on which to depend.

(v) *The first zygotic division*

We have been able to trace the main stages in the first division of the zygote nucleus. Where the broader end of the elongated nucleus rests against one pole of the zygote there appears an achromatic body; and below this assemble slender, intertwined chromatin threads arranged as loops (Fig. 22). Their number at this stage could not be counted with certainty. The nuclear membrane appears very thick and tends to show longitudinal ridges: possibly it has become wrinkled through loss of fluid from the nucleoplasm. Remnants of the degenerate karyosome lie below the part containing the chromatin threads. These threads condense, become beaded, and a number of discrete chromosomes are formed. At this stage these always appear double, and the number of pairs is seven (Fig. 23). The achromatic body divides and a spindle appears, with its ends resting against the pellicle of the parasite. The ends of the spindle sometimes appear more darkly stained than the rest, but there seem to be no centrosomes. In Fig. 24 the seven paired chromosomes are shown below the middle of the spindle. The nucleus elongates in the direction of the spindle's long axis, and its membrane begins to fade. Fig. 25 shows the

anaphase; there are seven chromosomes at each pole. Just how the members of a synaptic pair separate from one another at metaphase is not quite clear, but the appearances suggest that they remain attached to one another by one end for a time and are gradually pulled apart as the attachment thins out.

We have no doubt that reduction in this coccidian is zygotic, as in other coccidia where the phenomenon has been carefully studied.

(vi) *Sporogony*

We have seen no post-fertilization stage with two resting nuclei. And only once have we found the second nuclear division. This is depicted in Fig. 26, where two mitotic figures in anaphase are shown. In both, fibrillar differentiations are grouped at the poles, which lie superficially upon the zygote. Again the number of chromosomes at a pole is six or seven. From the appearance of this and of subsequent division stages it would seem that multipolar mitoses do not occur in the zygote of this coccidian.

After the second nuclear division, the mitotic figures, still unconnected one with the other, show only polar caps and lack the fibrillar differentiation (Fig. 27). The number of chromosomes is still seven. Unless an oocystic membrane is developed, the only way in which to distinguish the zygote at this stage from a male in process of microgamete formation is by noting the greater size of the dividing body and the different quality of the cytoplasm. (Care must be taken not to confuse with an oocystic membrane the lining of the vacuole in which a parasite develops: as the egg degenerates, this lining tends to thicken and it may come loose, as is shown in two of the figures on Pl. XXI.)

When nuclear division is ended, centripetal furrows cut into the cytoplasm (Figs. 11 and 12) and by this means numerous sporoblasts are delimited (Fig. 13), leaving no residuum. The number varies with the size of the zygote: it is common to find fifty. The nucleus of the sporoblast lies towards one pole: at first the seven chromosomes are distinct within it (Fig. 28), but this stage is followed by a resting phase with a reticulum, when sometimes a small karyosome appears (Fig. 29). The first nuclear division in the sporoblast may take place before the sporocyst is formed (Fig. 13), and naked sporoblasts with two dense nuclei are not uncommon in our preparations: but we have been unable to count the chromosomes in any division subsequent to sporoblast formation.

And once the sporocyst is formed it becomes extremely difficult to get clear pictures of the nuclei. The sporocyst is a transparent, doubly contoured envelope, with a completely smooth surface: sometimes it shows traces of an epicyst (Fig. 31). It seems very tough and resistant. The finished spore is elliptical or ovate in outline: the average measurements are $15{\cdot}5 \times 13{\cdot}5 \mu$. Exceptionally we have found spores nearly double this size, and these would presumably prove hyperzoic, as in *Aggregata*; but we have never seen any of them with their contents advanced beyond the binucleate stage.

Within all sporocysts the nuclei appear very darkly stained and almost homogeneous: often they have one border lobed and look as though just completing anaphase. For a long time we never found a spore with more than three nuclei (Fig. 30), and were coming to the conclusion that here, as in *Aggregata eberthi*, the ultimate number of sporozoites is normally three; but further material yielded normal-sized spores with four, six and even with as many as twelve nuclei (Figs. 31 and 32). Usually a vacuole lies in the midst: in life, this may contain a residual body, but unfortunately we have not observed living spores. Nor have we ever seen the finished sporozoites. That these are developed, however, before the spores are set free, is evident from the one picture of "*Monocystis thalassemae*" given by Lankester in the article referred to in the *Encyclopaedia Britannica*. This is a small outline drawing (dimensions not stated) of an elliptical spore in which are four (?) long slender sporozoites with what seem to be subterminal nuclei: in the legend below the figure is the note "chlamydospore of *Monocystis thalassemae* Lankester containing numerous falciform young". The "falciform young" in the picture occupy but a portion of the space within the spore, and one concludes that Lankester drew only such of the number as he could observe clearly throughout their length.

IV. MODE OF INFECTION

It seems obvious that the spores must escape when the worm spawns. They are protected less by the frail oocyst than by the tough membrane of the host egg. We cannot say how a new host becomes infected. It is possible, though unlikely, that the spores somehow enter the genital pouches through their outer apertures and hatch in contact with the eggs there. It is more probable, since *Thalassema* is a ciliary feeder, that the spores are ingested with fine food particles as these are swept back along the grooved proboscis, and that they hatch in the gut.

While studying the gregarines that inhabit the gut of *Thalassema neptuni* (Mackinnon & Ray, 1931 *a* and *b*) we cut many sections and examined the intestinal wall exhaustively; but we never saw anything there that resembled a stage in the development of the coccidian. We have also examined stained smears of the coelomic contents vainly. On one occasion, while looking at films of fresh blood from the coelom of a seemingly uninfected worm, we saw a few spindle-shaped bodies, measuring about $20 \times 3 \mu$, in the field: they glided along and moved the anterior end to and fro. It is not impossible that these were sporozoites of the coccidian on their way from the gut to the nephridial sacs.

We have never found the gonad infected, and presumably the sporozoites enter a nephridial sac either through its coelomic funnel or by burrowing through its wall after the eggs have been assembled within it. It is to be expected that the number of sporozoites reaching their destination will be small; and, as we have already indicated, the infection with schizonts is scanty.

V. Systematic position

The sporozoan parasite in the eggs of *Thalassema neptuni* is clearly not a gregarine, but a polysporocystid eimeriid coccidian with polyzoic spores. Following Hoare's (1933) classification, we should therefore place it in his subfamily Aggregatinae (family Eimeriidae). Hoare proceeds to use the number of sporozoites in the spore as the character diagnostic of aggregatine genera. On this basis, our parasite might possibly be regarded as a species of *Caryotropha*, for the indications are that its spores are dodecazoic. Moreover, in *Caryotropha mesnilii* (Siedlecki, 1907) schizogony and sporogony both occur in the same situation. But the microgametes of our coccidian resemble closely those of *Aggregata eberthi*, while the large vermiform adults are comparable rather with those of *Myriaspora trophoniae* (Lermantoff, 1913). In fact, no aggregatine genus hitherto described fits our particular case, and we feel justified in creating a new genus, *Ovivora*. *Monocystis thalassemae* Lankester therefore becomes *Ovivora thalassemae* (Lankester).

The following is a brief diagnosis of this, the type species:

Trophozoites large and vermiform, with one end spatulate when full grown: gametocytes spherical, the female considerably larger than the male: microgametes very numerous, elongate, biflagellate and having an undulating membrane: oocystic envelope feebly developed or absent: oocyst polysporocystid: sporocysts ovoid, $15{\cdot}5 \times 13{\cdot}5\,\mu$ *on the average, containing* 12(?) *sporozoites: sporogony and schizogony in the same host: merozoites very numerous and arising from the surface of a lobed schizont. Habitat: egg of* Thalassema neptuni *Gaertner at Plymouth.*

VI. Summary

1. An account is given of a sporozoan parasite, hitherto known as *Monocystis thalassemae* Lankester, and its coccidian nature is demonstrated.

2. Schizogony and sporogony both occur in the eggs of *Thalassema neptuni* while these are in the genital pouches (nephridial sacs). Schizogony was observed on three occasions, and only the later stages were seen.

3. The full-grown sexual parasites are vermiform and immobile. The males are smaller than the females.

4. The microgametocyte, when it becomes spherical, gives rise to very numerous, elongate microgametes, similar to those of *Aggregata*.

5. Fertilization has not been observed. The oocystic membrane is only sometimes formed and is always inconspicuous.

6. At all stages where a chromosome count was possible, the number of chromosomes was seven. The reduction division is zygotic. No polymitotic figures were observed either in microgametogenesis or in sporogony.

7. Numerous sporocysts are produced. These may contain as many as twelve nuclei, and presumably give rise to at least twelve sporozoites. The

formation of sporozoites has not been observed by us, but was noted by Lankester.

8. A new coccidian genus, *Ovivora*, is created for this organism, which now becomes *Ovivora thalassemae* (Lankester) and is relegated to the subfamily Aggregatinae in Hoare's classification.

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EXPLANATION OF PLATES XX–XXII

All figures, except Fig. 6, were drawn from sections and with the aid of a camera lucida. The material was fixed in Duboscq and Brasil's modification of Bouin's fluid, and stained with Heidenhain's iron-haematoxylin or with Delafield's haematoxylin and counterstained with chromotrop 2R.

PLATE XX

Fig. 1. Superficial section through a schizont, showing numerous nuclei, some of which are dividing. × 1000.

Fig. 2. Section through schizont covered with merozoites. × 1000.

Fig. 3. Merozoites on the surface of a schizont. × 2500.

Fig. 4. Young parasite, probably a sexual form, showing the nuclear structure characteristic of the early vermiform stage. × 2100.

Fig. 5. Older vermiform parasite, in which the nucleus has assumed the appearance usual in the adult phase. × 1000.

Fig. 6. Free-hand drawing of an egg containing two full-grown parasites, as seen under reflected light. × 500.

PLATE XXI

Fig. 7. Section through degenerating egg containing rounded-off male (small) and female (large) parasites. × 1000.

Fig. 8. Section of male and female parasites side by side within an egg. In the male, nuclear division is proceeding. (*Note.* The membranes indicated by lines surrounding the parasites are the linings of the vacuoles in which they develop.) × 1000.

Fig. 9. Male (*m*) and female (*M*) at a later stage. In this particular case, the male is unusually large and the female unusually small. In *m* the microgametes are forming on the periphery. *M* shows the fertilization spindle. Note degenerating microgametes alongside. × 1000.

Fig. 10. Four male parasites in one egg: (*a*) showing nuclei at the periphery; (*b*) microgametes with compact, elongating nuclei and sprouting flagella; (*c*) slightly later stage; (*d*) filiform, homogeneously staining microgametes breaking from the cytoplasmic residuum. × 1000.

Fig. 11. Multinucleate zygote. The peripheral nuclei are surmounted by slight, nipple-like elevations, and cleavage of the cytoplasm to form sporoblasts has begun. Note absence of oocystic membrane. The parasite lies within the remains of the emptied host egg. × 1000.

Fig. 12. A group of uninucleate sporoblasts in process of differentiation. Note absence of oocystic membrane. × 1000.

Fig. 13. Oocyst with sporoblasts. In some the first nuclear division has begun. In this specimen a delicate oocystic membrane has been formed around the group. × 1000.

PLATE XXII

(The host egg is omitted from all the following figures.)

Fig. 14. Middle portion of a vermiform parasite (female?) with its nucleus extruding siderophilous material from the karyosome. × 1400.

Fig. 15. Middle portion of a vermiform parasite (female?), showing the nucleus with emptied karyosome. × 1400.

Fig. 16. Rounded-off male, in which the nucleus is preparing for the first division. (Reconstructed from two sections.) × 2150.

Fig. 17. Section of male, showing four nuclei, one in anaphase. × 2150.

Fig. 18. Small portion of surface of male, in which nuclear division has just ceased. × 2150.

Fig. 19. Portion of periphery of male, showing two of the ultimate nuclei condensing and one anaphase pole. × 2150.

Fig. 20. Early stage in microgamete formation. (The membrane indicated by the black line is the pellicle of the parasite.) × 2150.

Fig. 21. Two maturing microgametes still attached to the cytoplasmic residuum. × 2150.

Fig. 22. The blunt, chromatin-containing pole of the fertilization spindle in a zygote. The achromatic body has appeared. × 2150.

Fig. 23. The first zygotic division. Paired chromosomes grouped below the achromatic body. (The two longest chromosomes are bent in **V** shape.) × 2150.

Fig. 24. The first zygotic division. A spindle has formed and the paired chromosomes are being drawn on to the equatorial plate. × 2150.

Fig. 25. The first zygotic division. Anaphase. In this specimen an oocystic membrane has formed. (Reconstructed from two sections.) × 2150.

Fig. 26. Second nuclear division in a zygote. Anaphase. (All but the ends of some of the chromosomes was in one section.) × 2150.

Fig. 27. Mitotic figure (anaphase) from periphery of a multinucleate zygote. × 2150.

Fig. 28. Sections of three sporoblasts in which the nuclei are entering on a resting phase. In the uppermost one the chromosomes can still be counted. × 1400.

Fig. 29. Section of sporoblast with resting nucleus. × 1400.

Fig. 30. Spore showing three nuclei. × 1800.

Fig. 31. Spore with four nuclei, one of which is dividing. × 1800.

Fig. 32. Spore with ten nuclei, some of which are dividing. × 1800.

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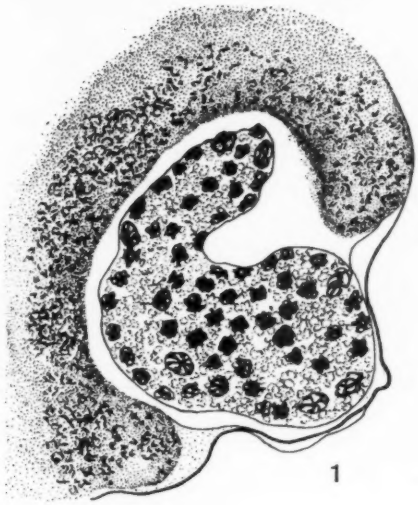

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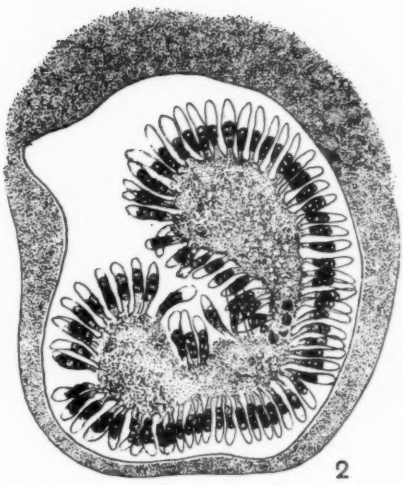

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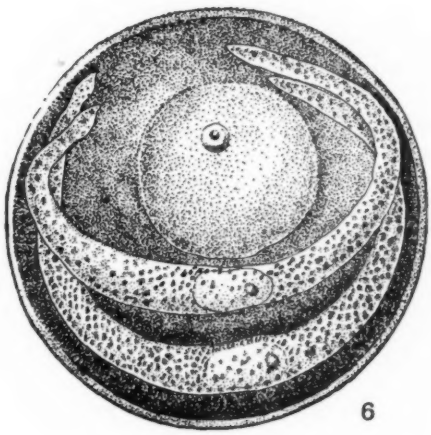

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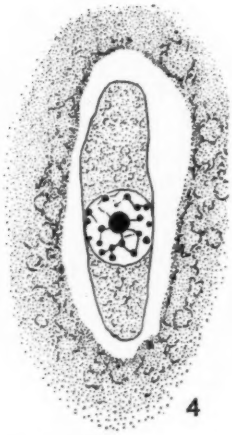

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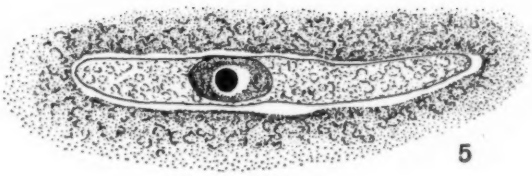

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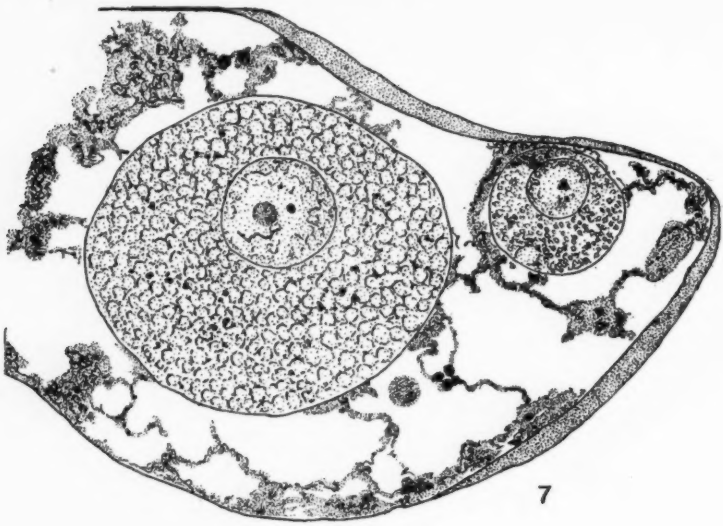

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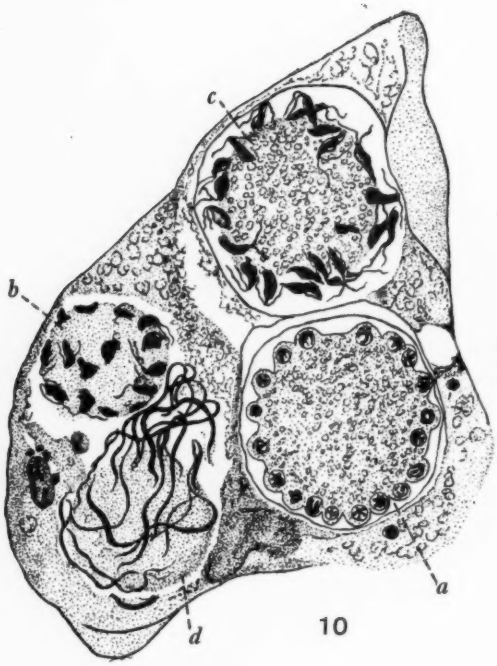

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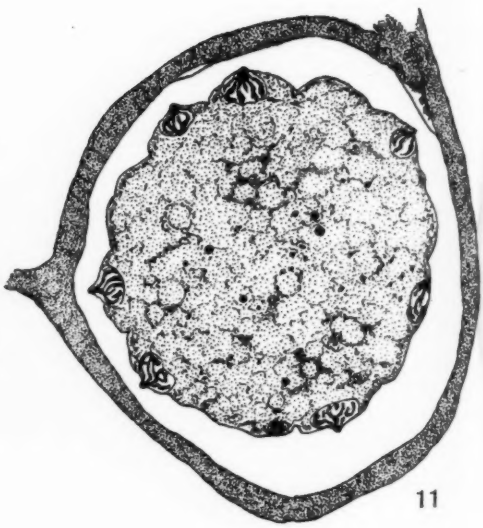

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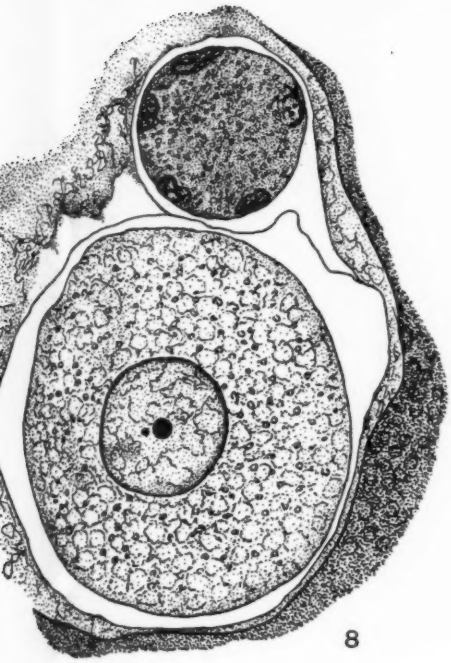

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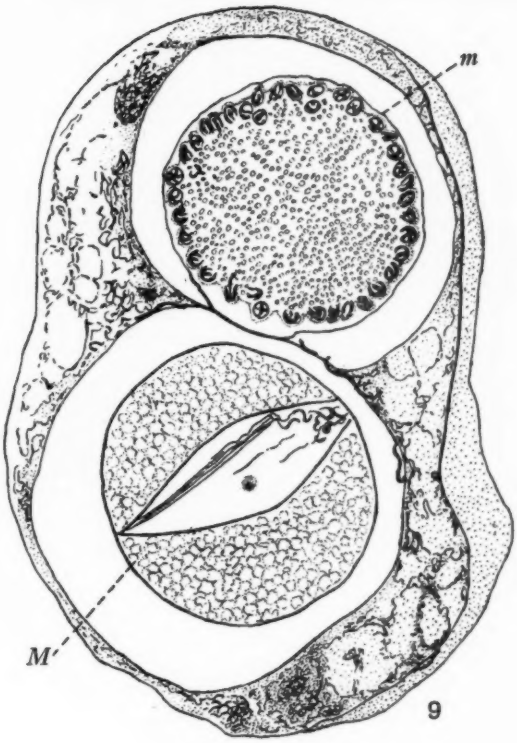

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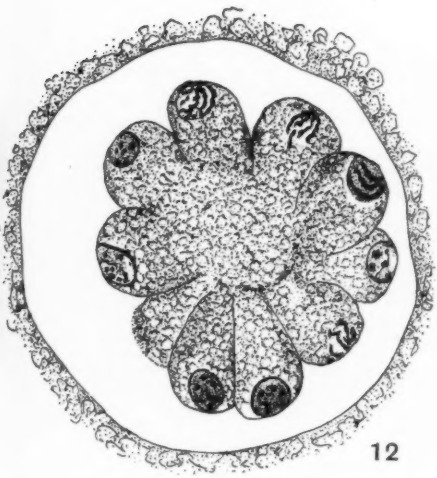

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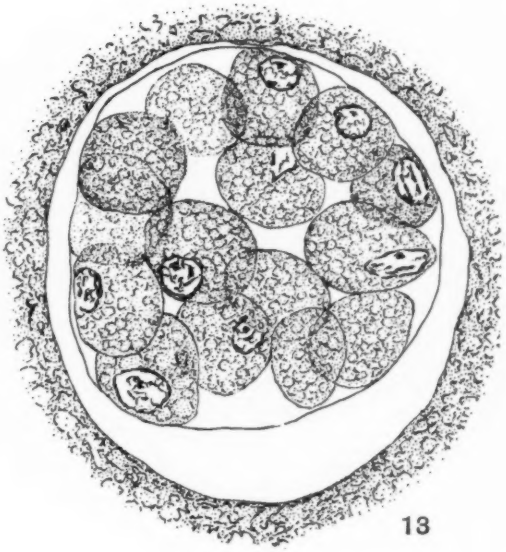

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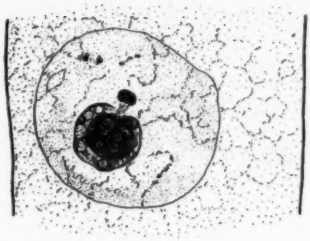

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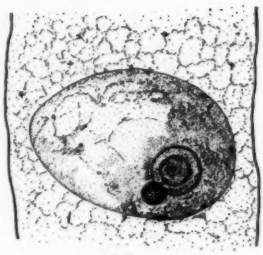

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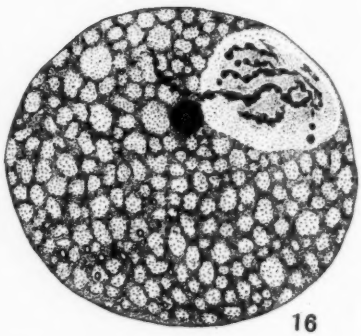

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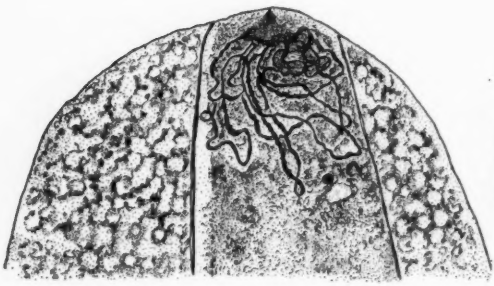

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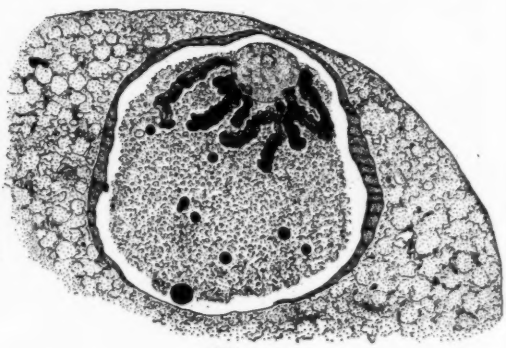

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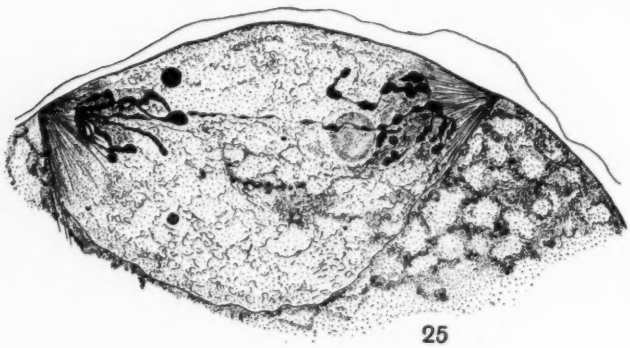

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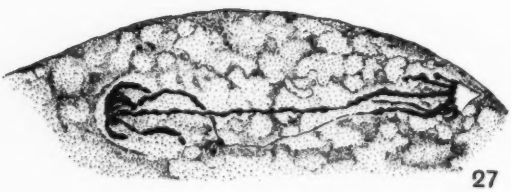

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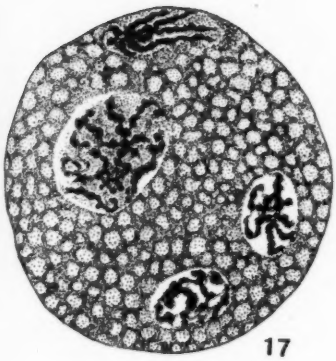

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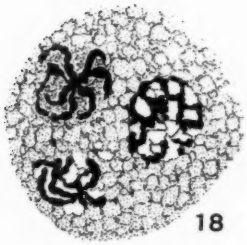

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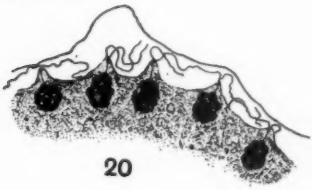

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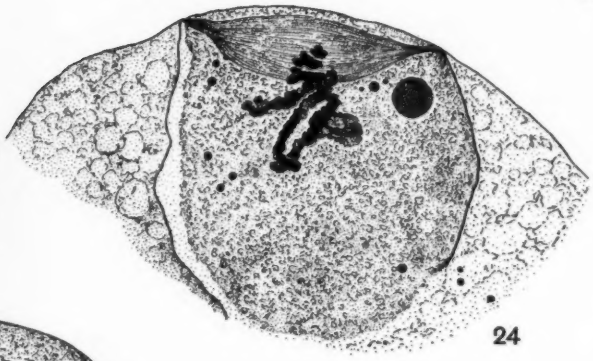

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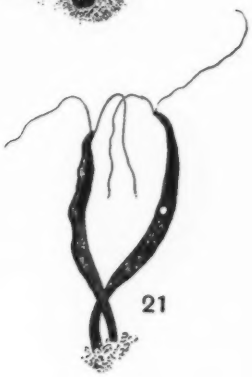

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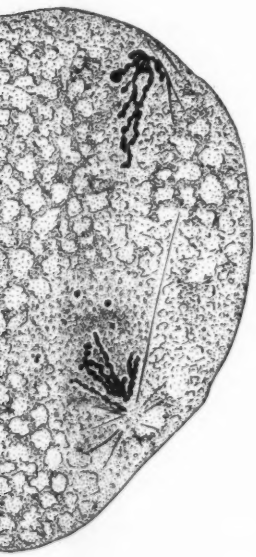

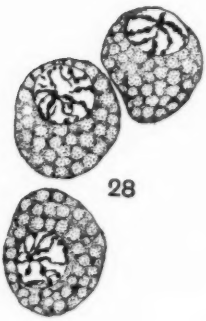

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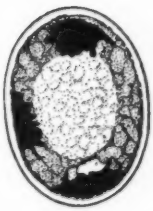

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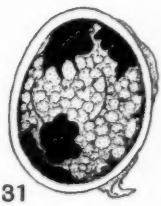

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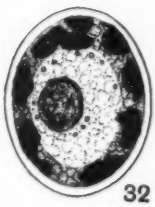

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THE HELMINTHS OF THE INTESTINAL CANAL OF MAN IN MAURITIUS; AND A FIRST RECORD OF *TRICHOSTRONGYLUS AXEI* LOCALLY

By J. LEWIS WEBB
Bacteriological Laboratory, Mauritius

(With 11 Figures in the Text)

The helminthic fauna of the intestinal canal of man in Mauritius can be split into the following already recorded worms:

(1) Cestoda. *Taenia saginata, Taenia solium, Raillietina madagascariensis,* and *Bertiella studeri.*

(2) Trematoda. No representative of this class of worms has been recorded from the intestines of man locally, though eggs of *Schistosoma haematobium* have been met with in the appendix, or occasionally are excreted in faeces.

(3) Nematoda. *Trichuris trichiura, Ascaris lumbricoides, Strongyloides stercoralis, Enterobius vermicularis* and *Necator americanus.* Eggs of the root-knot eelworm, *Heterodera marioni* (=*radicicola*) are not infrequently found during the examination of stools.

This work is an endeavour to ascertain the present status of the intestinal Strongylidae of man in this island.

Sandground (1929) and Van Slype (1934) have made use of the relative dimensions of the hookworm-like eggs in an attempt to detect other species of human intestinal Strongylidae; a similar method was adopted during the present investigation. Patients passing eggs which might not be those of *Necator americanus* were submitted to drug treatment with the object of recovering the adult worms.

This paper is thus composed of two parts:

A. The presumptive diagnosis by measurements of all hookworm-like eggs found in faeces of man.

B. The confirmation of the presumptive diagnosis by the collection and examination of adult worms, after drug treatment, in suspicious cases.

A. Measurements of hookworm-like eggs

For the purpose of classification the following figures collated from the papers of Sandground and Van Slype are given:

Necator americanus / *Ancylostoma duodenale*	58–68 × 39–47μ
Ancylostoma braziliense	Average 50 × 30μ
Ternidens deminutus	70– 94 × 47–55μ
Trichostrongylus colubriformis ...	73– 80 × 40–43μ
Trichostrongylus orientalis... ...	75– 91 × 39–47μ
Trichostrongylus probolurus ...	76– 80 × 43–46μ
Trichostrongylus vitrinus	84– 90 × 46–50μ
Trichostrongylus sp.? (Van Slype)	73– 80 × 37–42μ
Trichostrongylus sp.? (Sandground)	72–103 × 37–45μ

These authors further point out that a certain overlapping occurs in the measurements of the various eggs.

To avoid any risk of error only eggs whose dimensions do not come within the range of *Necator americanus* eggs were regarded as being those of other Strongylidae.

The technique adopted for the concentration of eggs in faeces during the survey was that used in a previous investigation. It has been fully described in the published account (Adams & Webb, 1934).

The eggs of local Strongylidae from man measured as follows:

Necator americanus...	55–73 × 34–50μ
Trichostrongyle	75–104 × 29–50μ
Ternidens deminutus	68–86 × 50–55μ
Ancylostoma braziliense	54–62 × 29–39μ
Trichostrongylus axei (intra-uterine)	71–78 × 36–39μ

Eggs from 336 samples of faeces were measured and the following results obtained:

331	samples or	98·5	per cent showed	*Necator americanus* eggs.
27	„	8·0	„	Trichostrongyle eggs.
3	„	0·9	„	*Ternidens deminutus* eggs.
3	„	0·9	„	*Ancylostoma braziliense* eggs.

The following eggs of Strongylidae occurred unassociated with those of other species:

Necator americanus	98·5	per cent or	331	samples
Trichostrongyle	1·2	„	4	„
Ancylostoma braziliense	0·3	„	1	„

Four out of the 27 samples showing Trichostrongyle eggs were unassociated with *Necator americanus* eggs; as pointed out by other workers, these eggs were very scanty; indeed, not more than 3–4 eggs were counted after concentration of about 1 g. of faeces.

From the present investigation the eggs in about 8 per cent of cases passing hookworm-like eggs were, after a careful study, diagnosed as those of Trichostrongyles; in Japan not less than 50 per cent of the hookworm-infested

people show a concurrent Trichostrongyle infestation; in the Belgian Congo about 10 per cent of the inhabitants were found Trichostrongyle-infested by Van Slype (1934): Lane, quoted by Manson-Bahr (1935), using the flotation technique in the detection of eggs in faeces, finds that Trichostrongyle eggs are commoner in the faeces of Ankylostome patients than has been supposed; Chandler, quoted by Manson-Bahr (1935) records them in 10 per cent of cases in Assam, and Manson-Bahr himself (1935) states that Trichostrongyle eggs are not infrequent in the stools of lascars in Kenya.

One of the Trichostrongyle infestations was observed in a child, 7 years old and born in Île de la Réunion. No *Necator* eggs were found. As his faeces were examined after only 5 days' residence in the colony, undoubtedly the infection was acquired in his own country.

The main characteristic of the *Ternidens* egg, according to Sandground (1931), is its short axis which is much broader than that of the hookworm egg; a study of the dimensions recorded obviously shows that we have met with 3 such cases.

B. THE COLLECTION OF THE ADULT WORMS AND THEIR IDENTIFICATION

Patients passing eggs regarded as not being those of *Necator americanus* were submitted to drug treatment with the object of recovering the adult worms.

Six patients supposed to harbour Trichostrongyles were given either carbon tetrachloride (40 minims) or oil of chenopodium (18 minims) or a mixture of both drugs; from two of these, adult Trichostrongyles were recovered as a result of the medication; the others failed to respond to the treatment.

One patient, after a dose of carbon tetrachloride, expelled a single female Trichostrongyle and some hundreds of *Necator americanus*; a week afterwards he was given a dose of chenopodium oil which caused him to pass a few more Necators but no Trichostrongyle. His faeces were examined a month later and typical eggs of the Trichostrongyle type were again found, with scanty large eggs of the *Ternidens* type. A new dose of carbon tetrachloride failed to dislodge any further worms. Thymol (40 grains) gave no better result.

A second patient expelled, after carbon tetrachloride treatment, two females and one male Trichostrongyle and several *Necator americanus*. His faeces, examined a month later, showed no more Trichostrongyle eggs.

A similar treatment applied to the Île de la Réunion patient was wholly unsuccessful.

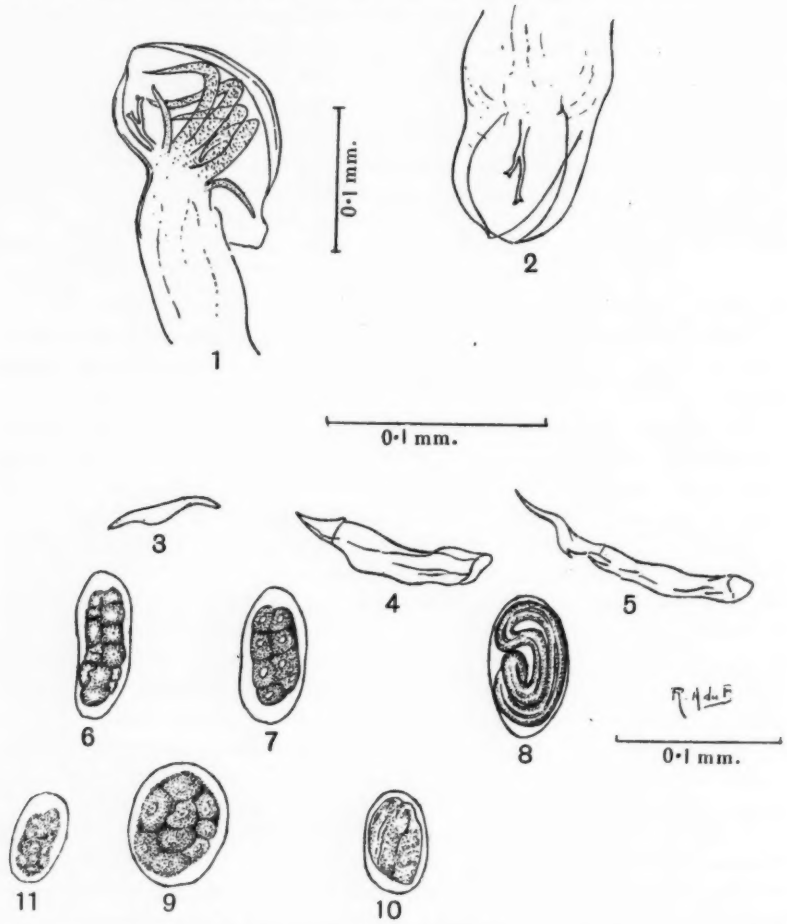
A dose of oil of chenopodium given to one of the *Ancylostoma braziliense* patients, an inhabitant of Rodriguez, who passed eggs of this type only, failed to dislodge any worms; a mixture of chenopodium oil and carbon tetrachloride and later pure carbon tetrachloride were equally inefficacious. It was found subsequently that he still passed eggs of the *Ancylostoma braziliense* type. Final proof that the worms were not *Necator americanus* is thus lacking.

Description of the worms

A. *Material from the second case*

One of the females was lost during manipulations; so the description will rest on the remaining female and the male.

The worms are fine and hair-like; larger at the posterior extremity and tapering gradually to the head end; they are of a dirty white colour.



Figs. 1–5. *Trichostrongylus axei* (♂), from Mental Hospital patient (Mauritius). 1. Bursa, left lateral view. 2. Bursa, dorsal view. 3. Gubernaculum. 4. Right spicule. 5. Left spicule.

Figs. 6–11. Human intestinal strongylid eggs (Mauritius). 6, 7, 8. Trichostrongyle eggs. 9. *Ternidens* egg. 10. *Necator americanus* egg. 11. *Ancylostoma braziliense* egg. (Eggs measured in concentrated salt solution; density 1200.)

The male measures 3·6 mm. long and 67·9μ broad in front of the bursa, which is divided into two lobes, each measuring 161 × 75μ; no separate dorsal lobe is seen. The bursal formula agrees fairly well with that given by Nagaty (1932) for *Trichostrongylus axei*; the ventro-ventral ray is thin and curved ventrally; it is of about the length and breadth of the externo-dorsal; the three lateral rays are bent inwards and are of about the same breadth; the postero-lateral is possibly narrower; the externo-dorsal is curved dorsally and comes to a level with the dorsal ray which measures 46μ in length. The cleft of the first bifurcation appears fairly deep with one branch roughly twice as long as the other; each branch is again bifid.

The head is 10·71μ wide and the excretory pore is at 114μ from the head end. The spicules are dissimilar, the left is the longer and measures 121μ in length; it shows the typical boot-shaped aspect characteristic of *T. axei*; the right one is broader and is 93μ long. The gubernaculum is 53μ and is situated dorsal to the right spicule; three concavities are seen when it is viewed laterally, two ventral and one dorsal; both ends terminate bluntly; the anterior end is longer and narrower than the posterior.

The female measures 3·8 mm. long with a maximum breadth of 61μ in the region of the vulva. The head is 10·71μ in diameter and the excretory pore is at 153μ from head end. The vulva is surrounded by thick cuticular lips and is sausage-shaped; it is 50μ long and is situated at 811μ from the tip of the tail. The uteri are divergent; the combined lengths of the ovejectors are 266μ. The anterior ovary bends backwards at 1·61 mm. from head end and the posterior bends forwards at 143μ from the tip of the tail. The distance of the anus from the tip of the tail is 75μ and the diameter of the body in the anal region is 25μ. The body tapers gradually and regularly from the loop of the posterior ovary to the tip of the tail and shows a slight elevation in front of the anus.

Intra-uterine eggs are thin-shelled and in the morula stage; they measure 71–78 × 36–39μ.

B. *Material from the first case; the single female*

It measures 5·314 mm. in length with a maximum breadth of 96·4μ in the region of the vulva. The diameter of the head is 11·78μ and the excretory pore is at 157μ from the head end. The vulva, whose lips are not so thick as those of the female above described, is crescentic and measures 64μ long; the distance of the vulva from the tip of the tail is 1·4 mm. The uteri are divergent and the combined lengths of the ovejectors are 428μ. The anus is situated at 78μ from the tip of the tail and the breadth of the body in the anal region is 36μ. The body after tapering for some distance narrows suddenly posterior to the anus, then tapers again gradually to the tip of the tail.

For the purpose of comparison, Tables I and II, drawn from Nagaty's work (1932) on the genus *Trichostrongylus*, give the dimensions of all species of Trichostrongyle recorded from man.

Table I

Male	Length in mm.	Max. breadth near bursa in μ	Diam. head in μ	Length right spicule in μ	Length left spicule in μ	Gubernaculum in μ
T. colubriformis	4·4–7·7	66–110	13–17	123–154	136–171	66–88
T. axei	2·6–3·7	44–66	8–13	74–96	96–123	52–61
T. probolurus	4·5–5·5	80	—	126–134	125–134	75–80
T. orientalis	3·8–4·8	72–79	—	119–133	119–133	65–85
T. axei (Mauritius)	3·6	67·8	10·71	93	121	53

Table II

Female	Length in mm.	Max. breadth near vulva in μ	Diam. head in μ	Length vulva in μ	Combined lengths ovejectors in μ
T. colubriformis	5·0–8·6	79–118	13–17	39–61	374–540
T. axei	3·3–4·2	44–61	8–13	44–57	202–281
T. probolurus	4·5–6·0	80	—	76	375
T. orientalis	4·9–6·7	75–83	—	—	—
T. axei (Mauritius)	3·8	61·0	10·71	50	266·0
Trichostrongylus sp.? (Mauritius)	5·3	96·0	11·78	64	428·0

A close comparison of the dimensions of the worms from the second case (A) with those of the other members of the genus shows that they fall within the range of the dimensions for *Trichostrongylus axei*; still further evidence is acquired from the shape of the bursal rays, the characteristic spicules and the gubernaculum in the male; the tip of the tail and the shape of the vulva in the female.

Undoubtedly, therefore, these worms are identical with *Trichostrongylus axei* (Cobbold, 1879), Railliet & Henry (1909).

The main differences between the female from case 2 and the single female from case 1 are the larger dimensions of the latter, the different shape of the vulva and that of the region posterior to the anus.

From Table II, 3 species have more or less the dimensions of the single female from case 1; but in the absence of a male it is impossible to identify this worm.

Treatment. In general Trichostrongylosis in man is considered unimportant from a medical standpoint, because the infestations hitherto recognized have been light; but gross infestations would be liable, as in animals, to give rise to severe secondary anaemia.

Rodhain (1930) has observed a case of anal itching in a European caused by a Trichostrongyle.

In Mauritius, no particular symptom attributable to the Trichostrongyles was noted, except possibly in case No. 1; the patient passed large amounts of pure blood, which could be assigned to no particular ailment; anyhow, it is very unlikely that Trichostrongyles could be responsible for such blood effusion.

The literature on the treatment of Trichostrongylosis is conflicting: *Trichostrongylus orientalis* is stated by Nagaty (1932) to be easily dislodged by carbon tetrachloride; Manson-Bahr (1935) cured two patients in Kenya of their *T. colubriformis* infestation by carbon tetrachloride, whilst Sandground (1929), in Southern Rhodesia, failed to recover any Trichostrongyle from his patients treated with carbon tetrachloride (4 c.c.) and carbon tetrachlorethylene (5 c.c.); Van Slype (1934) was unsuccessful in dislodging these worms from his patients in the Belgian Congo; Kalantarian (1934) successfully treated an Armenian with thymol.

These results show that a partial eradication of Trichostrongyles is obtained when carbon tetrachloride is employed.

SUMMARY

1. Systematic measurements of all hookworm-like eggs from the faeces of 336 patients in Mauritius led to the finding of 8 per cent Trichostrongyle, 0·9 per cent *Ternidens deminutus*, and 0·9 per cent *Ancylostoma braziliense*-like eggs.

2. This percentage of Trichostrongyle eggs includes one case from an inhabitant of the French colony, Réunion.

3. Hookworm eggs of a very small size, possibly *Ancylostoma braziliense* were found unassociated with the typical *Necator americanus* eggs, in the faeces of an inhabitant of Rodriguez; the adult worms appeared drug-resistant.

4. A partial eradication of the Trichostrongyles was obtained in one case, and an apparently complete eradication in another, of 6 patients treated with carbon tetrachloride.

5. The Trichostrongyles expelled by one of the patients were identified as *Trichostrongylus axei* (Cobbold, 1879) Railliet & Henry (1909).

6. No particular symptoms which could be ascribed to the action of the Trichostrongyles were observed in any of the affected patients.

7. Drugs administered orally to a patient passing *Ternidens deminutus*-like eggs failed to dislodge any of his worms.

ACKNOWLEDGEMENTS

I desire to express my deep sense of gratitude to the Director of the Medical and Health Department, Dr J. Balfour Kirk, for the great interest he has shown, and facilities afforded to me, throughout the course of this work.

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A MATHEMATICAL ANALYSIS OF SUPERPARASITISM BY *COLLYRIA CALCITRATOR* GRAV.

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(With 2 Figures in the Text)

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I. Introduction

The term "superparasitism" was introduced by Fiske (1910) to denote the state "when an individual host is attacked by two or more species of primary parasites, or by one species more than once". It now has the more restricted meaning—the condition resulting when an individual host insect is attacked by a superabundance of one species of parasite. Fiske stated further that "the prevalence of superparasitism depends entirely upon whether or not the female parasite is gifted with a prescience which will enable her to select healthy hosts for her offspring". From his observations on various parasites, particularly those of the gipsy moth, he came to the conclusion that, as a rule, this faculty was non-existent, and suggested that in such a case the distribution of parasite eggs among the hosts would be governed by the laws of chance.

Thompson (1924) developed the mathematical aspect of Fiske's idea, and showed that if the parasite eggs were distributed at random among the hosts then the amount of parasitism expected is expressed in its simplest form by the equation

$$y = N\,(1 - e^{-x/N}),$$

where N is the total number of hosts, x the number of parasite eggs distributed, and y the number of hosts parasitized.

Up to this point, superparasitism, although frequently found in the field, had not been made the subject of any detailed observations. However, when Salt (1932), in the course of his investigations of the wheat-stem saw-fly,

Cephus pygmaeus Linnaeus, found considerable natural superparasitism by the ichneumonid parasite *Collyria calcitrator* Gravenhorst, he attempted an analysis of the results of some 4000 dissections of saw-fly larvae in order to test the validity of the random distribution theory. He concluded that when *Collyria* attacks *Cephus*, the females do not distribute their eggs at random among the hosts, but that they exercise some degree of discrimination. No alternative suggestion was offered at the time to explain in what way the parasite's discriminative faculty might work.

When an investigator tries to reveal an insect's behaviour by means of an experiment, the details of time, temperature, etc., are all known to him, and he can correlate them usefully with his results, unless, of course, the artificial environment has caused the creature to react quite abnormally. On the other hand, the natural environment of the field is composed of so many varying factors that it is impossible to account for each one, far less to give it its true significance. Nevertheless, the truth is more likely to be found in the field than in the Petri dish.

It was this realization of the greater importance of field data which suggested to the writer that the results of Salt's work on *Cephus* and *Collyria* might provide a suitable starting-point for a further investigation of the parasite's behaviour. The *Cephus* larvae which Salt examined were drawn at random from a very much larger collection, and can therefore be taken as a typical field sample. Considered by themselves, the figures of the distribution of the *Collyria* larvae among the *Cephus* did not explain how the adult parasites had gone about the business of choosing suitable hosts to attack. To analyse them in relation to such details as are relevant of the life histories of both insects seems more promising.

The aim, then, of the following paragraphs is to draw up some kind of programme of the activities of *Collyria calcitrator* which will account for the observed distribution of that parasite in its host *Cephus pygmaeus*. The method is to use, as far as possible, what is already known about the two insects, and then, where facts are not available, to resort to hypotheses. Theories unsupported by observation can be dangerous, and one which claims to answer the question of what the female *Collyria* does when she comes to an already parasitized host is no exception. We can only guess the working of an insect's "mind", and in our choice of faculties with which to invest her we must remember that hypotheses which give the desired result are not necessarily facts. Their main value is that they suggest in what direction we should look for further evidence with which to solve the problem.

II. Life history of the wheat-stem saw-fly

There is only one generation in the year of the saw-fly *Cephus pygmaeus*. In England the adults are seen towards the end of June and in the beginning of July. The eggs are laid generally between the third and fourth nodes and inside the lumen of the developing wheat-stem, the female sawing a small

opening through the plant tissues with her ovipositor. The middle of the day is the period of greatest egg-laying activity. In a period of from 7 to 10 days the egg hatches and the larva proceeds to eat its way through the interior of the stalk. Ries (1926) was of the opinion that during its growth period the larva traversed the stem several times, and in his field observations Mr H. S. Hanson found that the first movement of the larva on hatching is to travel upwards almost to the ear. After about a month, when the larva is full-grown, it arrives at the base of the stem. Here it prepares itself for the winter resting state. About an inch above the root the creature gnaws round the inside of the stem, and so weakens it that it is easily broken over by a strong wind or even a heavy shower of rain. Below the groove the stem cavity is sealed with a plug of frass, and in the small chamber so formed the cocoon is spun. The larva remains quiescent in its cocoon throughout the winter and in the following May pupates. After metamorphosis it bites its way out through the plug (Ries, 1926).

III. PARASITES OF *CEPHUS*

In his comprehensive study of *Cephus pygmaeus* in England, Salt (1931) recorded 13 parasite species reared by him from material examined. Here is his list:

"The primary parasites and their frequence per hundred *Cephus*-infested stalks are:
Hemiteles hemipterus, Fabricius (ICHNEUMONIDAE, Cryptinae); 0·66.
Leptocryptus bellulus, Kriechbaumer (ICHNEUMONIDAE, Cryptinae); 0·02.
Microcryptus (?) *unifasciatus*, Schmiedeknecht (ICHNEUMONIDAE, Cryptinae); less than 0·0001.
Pezomachus fallax, Foerster (ICHNEUMONIDAE, Cryptinae); less than 0·001.
Gambrus tricolor, Gravenhorst (ICHNEUMONIDAE, Cryptinae); less than 0·001.
Pimpla detrita, Holmgren (ICHNEUMONIDAE, Pimplinae); 2·12.
Collyria calcitrator, Gravenhorst (ICHNEUMONIDAE, Pimplinae); 62·25.
Microbracon terebella, Wesmael (BRACONIDAE, Braconinae); 2·77.
Pleurotropis benefica, Gahan (CHALCIDIDAE, Eulophinae); 3·95.

One species attacks *Hemiteles hemipterus* as a secondary parasite:
Hemiteles inimicus, Gravenhorst (ICHNEUMONIDAE, Cryptinae).

Four species attack *Microbracon terebella* as secondary parasites:
Hemiteles hemipterus, Fabricius (ICHNEUMONIDAE, Cryptinae).
Pezomachus terebrator, Ratzeburg (ICHNEUMONIDAE, Cryptinae).
Eurytoma appendigaster, Swederus (CHALCIDIDAE, Eurytominae).
Habrocytus sp., (CHALCIDIDAE, Pteromalinae)."

Since none of the secondary parasites attacks *Collyria* there is no need to deal further with them in this discussion, but concerning the primary parasites the following points are worth considering:

(1) *Collyria calcitrator*. This is the only ichneumonid known to oviposit in insect eggs. In late June and early July the females may be seen ovipositing in the wheat-fields, evening, according to Zolotarevsky (1915), being the time preferred. In the words of Salt: "Their usual procedure is to alight near the top of a stem, a few inches below the ear, and to move downwards, head first,

examining the stalk with their antennae. It is possible that they, like many other parasites, have the ability to sense their host through the tissues of the plant, but this ability would not seem to be essential because the scar made by the ovipositing saw-fly is visible even to human eyes." The egg is the only stage of the host known to be attacked (Kurdjumov, 1915; Smith, 1931). The parasite eggs are deposited inside those of the host, and the larvae develop inside those of the host larvae. At first, the *Cephus* appears to suffer no serious injury from the presence of the parasite, and the larva, usually looking quite healthy, is able to form its hibernaculum at the base of the stem in the usual way. However, in the spring the parasite increases rapidly in size at the expense of its host, which is devoured, all except the skin. Pupation takes place in May, inside the host's cocoon, and the adult *Collyria* emerges in June.

(2) *Hemiteles hemipterus*. The female parasite attacks the full-grown larva of the host. She pierces the cocoon with her ovipositor and deposits an egg on the larva, which she first of all paralyses. The parasite forms its cocoon inside that of the saw-fly.

(3) *Leptocryptus bellulus*. This parasite's egg has not been observed, but since it is said to be very difficult to distinguish between the various larval stages of *Leptocryptus* and those of *Hemiteles hemipterus*, the suggestion is that the two series of attacks occur about the same time, i.e. that in the case of *Leptocryptus*, too, the full-grown larva of the host is attacked.

(4) *Microcryptus* (?) *unifasciatus*.

(5) *Pezomachus fallax*.

(6) *Gambrus tricolor*.

The above three are of such rare occurrence as to be negligible. In each case the host larva at the base of the wheat-stem is replaced by a cocoon similar to that of *Hemiteles*.

(7) *Pimpla detrita*. The *Pimpla* larva is found generally above the second node of the stalk, showing that the host larva is attacked in its early stages. The female *Pimpla* lays her eggs externally on the *Cephus* larvae, which are first of all paralysed, and when the parasite larvae emerge they remain beside the food supply. When a larva is full grown only a few scattered particles of its host remain. Because of its habit of attacking the host larva before the latter has achieved its descent of the stem the parasite is destroyed in large numbers in the straw when the wheat is cut.

(8) *Microbracon terebella*. Four or five larvae of the parasite *Microbracon* can be supported by one *Cephus* larva. The parasites feed externally on their host, which is, as a rule, not killed until after it has completed its hibernaculum. The small parasite cocoons are then spun inside that of the saw-fly, filling the cavity beneath the plug of frass.

(9) *Pleurotropis benefica*. In regard to *Pleurotropis*, Salt says: "I have not observed the oviposition or seen the egg of this species. The youngest individuals examined were dissected from the body cavity of larvae of *Cephus pygmaeus* on 15 July 1930." And again: "By the middle of August 1930, only mature

larvae of the parasite were found. At that date most of them were still enveloped in the skin of their host, but this covering was soon pushed to the bottom of the hibernaculum. In this state, without spinning any cocoon, the larvae pass the winter." No hyperparasites are known.

IV. *Collyria* in relation to other parasites of *Cephus*

Of the 9 parasites of *Cephus pygmaeus*, 3 can be neglected because of their extreme rarity, 2, *Collyria* and *Pleurotropis*, are endoparasites, and 4, *Pimpla*, *Hemiteles*, *Leptocryptus* and *Microbracon*, are ectoparasites. To the ectoparasites, preying on their hosts externally, it makes no difference whether an internal parasite is present or not, so long as the *Cephus* larva appears to be in a healthy condition. In actual fact, in the case of the first 3 species mentioned, head capsules of *Collyria* have been found along with the host remains. To use the term defined by Smith (1929) they are intrinsically superior to *Collyria*, and no doubt the same is true of *Pimpla*. *Pleurotropis*, on the other hand, is intrinsically inferior to *Collyria*, for if both are present in a *Cephus* larva the latter survives. Why this should be is not exactly known, but possible reasons are (*a*) that if *Collyria* is an egg-parasite, its larva has the advantage of time and devours the younger *Pleurotropis* larva or the egg before it hatches, (*b*) the *Collyria* larva may have the more powerful jaws of the two, (*c*) that the secretions of the *Collyria* larva may be toxic to *Pleurotropis*.

With regard to the distribution of *Collyria* in the host the points of importance in the above are as follows: The examination during the winter of *Cephus*-infested stubble will yield healthy host larvae, host larvae containing *Collyrias*, larvae of *Pleurotropis*, and, finally, larvae of the various ectoparasites. Now since *Pleurotropis* cannot survive in the presence of *Collyria*, each *Pleurotropis* larva must have come from a host which was not previously attacked by *Collyria*. On the other hand those hosts which in the stubble have been replaced by the ectoparasites may have been healthy when attacked by them, or they may already have contained an endoparasite, and presumably the distribution of *Collyria* in the hosts they have failed to attack is similar to the distribution in those they have devoured. In the same way the *Cephus* larvae which are destroyed by moulds and fungi are infected independently of any parasites they may contain.

The position, then, is this: as the result of handling large quantities of material from various localities and in two different seasons, Salt (1931) estimated that on an average:

Moulds killed	2·97 per cent of the larvae
Ectoparasites (*Hemiteles*, *Leptocryptus*, *Pimpla* and *Microbracon*) killed a total of	5·57 per cent of the larvae
Pleurotropis killed	3·95 per cent of the larvae
And that the remaining	87·51 per cent of the larvae were apparently healthy

Concerning the latter he says: "When, however, these apparently healthy larvae were dissected very many of them were found to contain the larvae of

an endophagous ichneumonid, *Collyria calcitrator*. Out of a total of 5015 random dissections this parasite was found in 3567 larvae, or 71·13 per cent. Since the larvae obtained represent only 87·51 of the actual infestation, however, the effective parasitism of *Collyria calcitrator* is 62·25 per cent of the entire *Cephus* population." Therefore, when he (Salt, 1932) says: "To determine the frequence of superparasitism by *Collyria calcitrator*, 3761 larvae of *Cephus pygmaeus* were dissected. Of these, 2712 or 72·11 per cent were parasitized by *Collyria*", he has omitted to allow for the fact that in the stubble there are approximately 3·95 cocoons of *Pleurotropis benefica* for every 87·51 *Cephus* larvae, or 149 for 3761 larvae, and that these cocoons, because of *Pleurotropis*' intrinsic inferiority, must represent hosts unparasitized by *Collyria*. The second column of Table I shows Salt's observations, while the third gives the correction for the effect of *Pleurotropis*. The change, though only a slight one, nevertheless reduces whatever degree of discrimination *Collyria* may be supposed to possess.

Table I

No. of parasites in a host	Observed no. of hosts	Suggested correction to include hosts eliminated by *Pleurotropis*
0	1049	1198
1	2195	2195
2	332	332
3	98	98
4	49	49
5	18	18
6	7	7
7	4	4
8	5	5
9	2	2
10	0	0
11	1	1
12	0	0
13	0	0
14	0	0
15	0	0
16	1	1
Total	3761	3910

V. The emergence of *Collyria* in relation to the activity of *Cephus*

In the case of hosts in which only one parasite can survive, superparasitism may be due to a scarcity of hosts or to the female parasites' inadequate ability to select healthy material from among the hosts which have previously been attacked, or to a combination of both factors. When a laboratory experiment is used to decide whether parasites distribute their eggs at random, the hosts can be supplied in sufficient numbers to rule out any chance of shortage. In analysing field material, on the other hand, one must investigate the possibility that at some period in the season of parasite activity the hosts are relatively scarce; and if it is the case, one must try to assess the superparasitism so caused, before attempting to measure that resulting from the parasite's natural powers of selectivity.

The present problem concerns us with the distribution of nearly 4000 parasites in a similar number of hosts, which were picked at random and can be taken as representative of a very much larger collection of material. The dissections showed that not only was there superparasitism in an appreciable fraction of the hosts, but that this superparasitism could occur in an extreme degree, 7, 8 and even more parasites being found in a single host. That some at least of this superparasitism might be due to a scarcity of *Cephus* eggs at a time when relatively large numbers of female *Collyria* were searching for hosts to attack, was suggested by Salt's observations on the emergence of adult parasites from a sample of infested wheat-stubs. This was kept in an unheated insectary and the emergents removed and counted daily. The results were recorded as a graph (Salt, 1931, p. 517), which shows that *Collyria* starts to emerge at least a week earlier than its host, and that in both cases emergence continues over an interval of a month. Now if all the insects in this sample had been permitted to live to the extent of their natural lives, what would have been the daily aggregates of host and parasite? Unfortunately there are no records of the longevity of either *Collyria* or *Cephus*. But it is known that in captivity females of various saw-flies will lay all their eggs in about a week, and that when oviposition ceases they die. Also many ichneumonid parasites survive for a month and more in captivity. In the field the expectation of life must be shortened because the insects are being continually preyed upon by birds, etc., and so averages of 6 days for *Cephus* and 25 for *Collyria* were taken to be reasonable estimates for the length of adult life. Table II, which was compiled from the graph mentioned above, was based on these assumptions. In Fig. 1, the numbers of *Cephus* and *Collyria* are seen to form two fairly symmetrical curves.

The next step is to represent the general case of emergence in the field. Salt found that in the insectary emergence began about 2 weeks earlier than in the field, evidently because the temperature had been slightly higher than the ground temperature outside. Since presumably the insects would have completed their development in the same order had they been left in their natural environment, all that is necessary is to add 14 days to the dates in Fig. 1, so that 19 May becomes 2 June, and so on. Again, Fig. 1 illustrates what might have happened with a particular sample. It will be better to work with a more general case, for which are suggested the smooth symmetrical curves also shown in the figure. Finally, it must be remembered that the present problem is concerned with the number of females rather than with the total number of insects, for the number of host eggs available on any day will depend on the number of female *Cephus* alive, while the number of female *Collyria* will determine how many parasite eggs are distributed. For both *Cephus* and *Collyria* it is known that the females start to emerge a few days later than the males, and in either species the females form roughly 60 per cent of the population. This rather lessens the probability of a serious error arising from the fact that the information published does not give details of

Table II

Date	No. of *Collyria* emerging each day	No. of *Collyria* alive (adult lives 25 days)	No. of *Cephus* emerging each day	No. of *Cephus* alive (adult lives 6 days)
May 19	1	1	—	—
20	0	1	—	—
21	1	2	—	—
22	2	4	—	—
23	2	6	—	—
24	6	12	—	—
25	6	18	—	—
26	7	25	—	—
27	13	38	—	—
28	23	61	—	—
29	24	85	2	2
30	18	103	1	3
31	30	133	0	3
June 1	31	164	1	4
2	38	202	2	6
3	14	216	0	6
4	86	302	13	17
5	55	357	16	32
6	51	408	19	51
7	24	432	9	59
8	23	455	10	67
9	23	478	10	77
10	30	508	4	68
11	38	546	39	91
12	20	566	45	117
13	8	573	25	133
14	5	578	19	142
15	5	582	18	150
16	2	582	7	153
17	2	582	35	149
18	3	579	27	131
19	3	576	4	110
20	—	569	18	109
21	—	556	9	100
22	—	533	9	102
23	—	509	0	67
24	—	491	1	41
25	—	461	12	49
26	—	430	16	47
27	—	392	4	42
28	—	378	4	37
29	—	292	2	39
30	—	237	—	38
July 1	—	186	—	26
2	—	162	—	10
3	—	139	—	6
4	—	116	—	2
5	—	86	—	—
6	—	48	—	—
7	—	28	—	—
8	—	20	—	—
9	—	15	—	—
10	—	10	—	—
11	—	8	—	—
12	—	6	—	—
13	—	3	—	—

the sexes separately. In Fig. 2 are reproduced the smooth curves of Fig. 1 with the difference that the date of origin is altered from 19 May to 8 June, 14 days to allow for the difference between field and insectary conditions and 6 days to represent the later appearance of the females.

The relative numbers of adult hosts and parasites on successive days of the season of activity are represented by the corresponding ordinates of the two curves in Fig. 2; and this diagram, even if, through the lack of appropriate data, it is far from accurate at least illustrates how much the ratio between the numbers of *Cephus* and *Collyria* may vary.

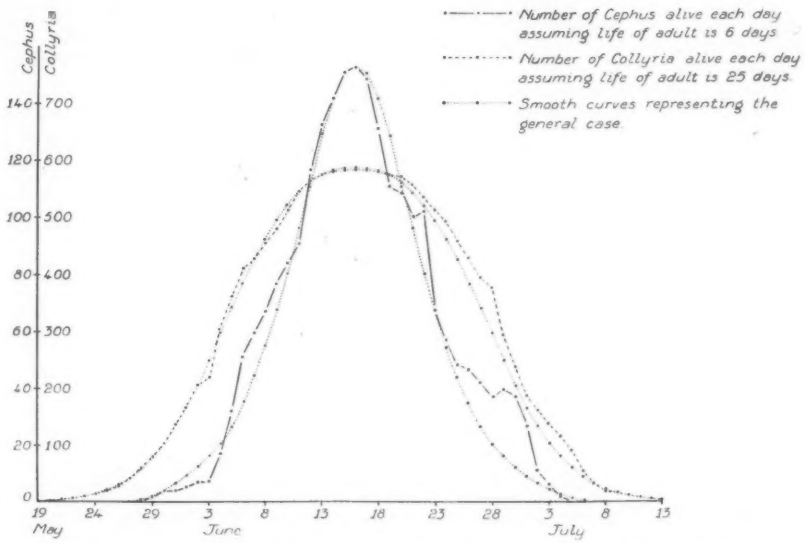

Fig. 1. *Cephus* and *Collyria* populations estimated from a sample of wheat-stubble.

The ordinates of the curves give the numbers of mature adult female insects alive on any given date. They are therefore, on the average, proportional to the number of eggs laid on that day. Thus a female *Cephus* can produce about 50 eggs, or an average of 9 a day, so that 2 hosts on 18 June represents 18 host eggs, 153 on 6 July represents 1377, and the rest in the same proportion. It will be seen later on, however, that the ratios between the values are of more importance than the actual numbers indicated by the scale of the graph. In the same way one would expect the numbers of *Collyria* eggs distributed on the various days to be roughly proportional to the numbers of female *Collyria* with the exception that up till 17 June there can be no *Collyria* eggs because there are no *Cephus* eggs. At first sight there appears to be a similar period at the end of the season, from 26 July till 12 August, but it should be remembered that a *Cephus* egg takes 8 or 9 days to hatch, so that

there is still a certain number of host eggs available after the last few of the adult *Cephus* have died.

VI. The effect of cutting the wheat

As described above, the *Cephus* larva traverses the interior of the wheat-stem, and when full-grown makes its hibernaculum an inch or so above the root. Since larval development takes nearly a month, it follows that if the wheat is cut in the latter part of August, a certain proportion of *Cephus* will

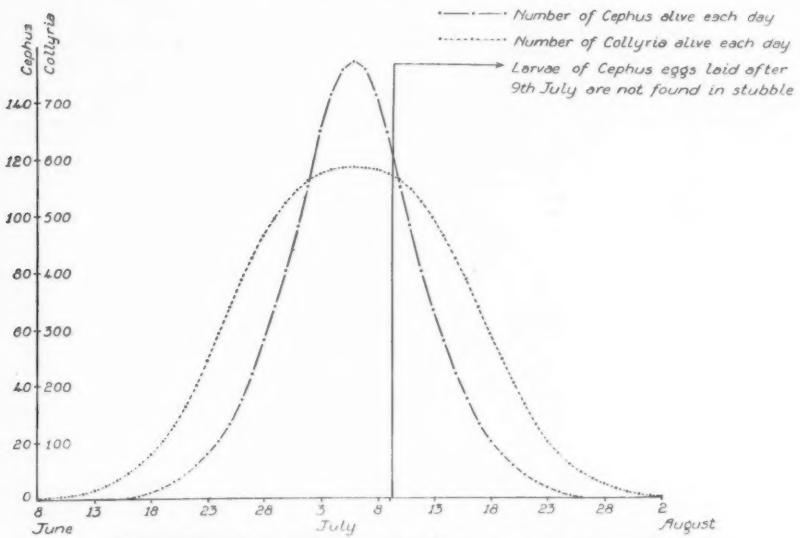

Fig. 2. General case of *Cephus* and *Collyria* populations in the field.

not have reached the level at which the stems are cut, and are therefore not found in the stubble. The point not to be overlooked is that the proportion of parasites distributed among the hosts in the stubble may be different from that in the hosts which are removed with the straw. To overcome this difficulty, the examination of the distribution of parasites must be confined to the earlier part of the oviposition period, and as nearly as can be judged to that fraction of it concerned with the *Cephus* larvae which can be estimated to have had time to reach the bottom of the stems by the time the wheat is cut.

Salt (1931) examined a sample of 90 infested wheat-stalks on the day of the cutting of the wheat. He found that in 21 of them the *Cephus* larva or its parasite (*Microbracon* or *Pimpla*) was still above the level of cutting. These *Cephus* larvae were not examined for *Collyria* but in any case such a small number could not have supplied reliable information. Still, the fact that the stubble contains $\frac{69}{90}$ of the *Cephus* population can be utilized in the following way. In Fig. 2 the total number of host eggs is represented by the sum of th

ordinates for each day unit of the *Cephus* curve. This amounts to 2163; and $\frac{69}{90} \times 2163 = 1658$, which approximates to the sum of the ordinates up to and including 9 July; i.e. the number of host eggs laid by the end of 9 July. As shown in the first two columns of Table III, the total number of host eggs laid from 17 June to 9 July is 1580. Now the number of hosts actually under investigation is 3910 which is $1580 \times 2{\cdot}475$, and so the multiplication of each item in the second column by the factor 2·475 gives the required order of appearance as eggs of the host individuals in the stubble.

Table III

Date	No. of hosts from graph	Corresponding arrangement of 3910 hosts
June 17	1	2
18	2	5
19	4	10
20	6	15
21	9	22
22	12	30
23	16	39
24	20	49
25	26	64
26	35	86
27	44	108
28	55	136
29	66	163
30	80	198
July 1	97	240
2	110	272
3	129	320
4	142	352
5	151	374
6	153	379
7	151	374
8	142	352
9	129	320
Total	1580	3910

The corresponding arrangement of the 3600 parasites is not quite so straightforward. The number of parasite eggs laid per day will be proportional to the number of adult *Collyria* alive. That is, as before, it will be proportional to the ordinates of the *Collyria* curve in Fig. 2 from 17 June onwards, but the exact figures are found to vary slightly according to the way in which the parasite is assumed to choose the hosts she attacks.

VII. HYPOTHETICAL PARASITE DISTRIBUTIONS

The stage has now been reached at which it is possible to calculate theoretical distributions according to various hypotheses of discrimination and lack of it. The aim is of course to find the theoretical case which most closely corresponds to the distribution actually observed for *Collyria*, and then to decide whether the assumptions on which it is based are acceptable.

To begin with we will consider what happens in the case of an insect which can discriminate perfectly between parasitized and healthy hosts. In Table IV are given the numbers of female parasites active each day, numbers which,

as has been pointed out, are proportional to the numbers of parasite eggs laid daily. From 17 June to 9 July they total 9056, and when each is multiplied by the factor 0·398, give a series which for that period has the sum 3600 (third column). The next column shows the numbers of host eggs laid on the corresponding days. It is plain that for the first 3 or 4 days intense super-

Table IV

Date	No. of parasites from graph	Corresponding arrangement of 3600 parasites	No. of hosts	Arrangement of parasites to give 3600 in hosts	Parasite distribution
June 17	61	24	2	22	2 ♂11
18	80	30	5	28	3 ♂6, 2 ♂5
19	102	40	10	38	8 ♂4, 2 ♂3
20	131	52	15	50	5 ♂4, 10 ♂3
21	164	65	22	63	19 ♂3, 3 ♂2
22	202	79	30	76	16 ♂3, 14 ♂2
23	244	96	39	93	15 ♂3, 24 ♂2
24	288	114	49	110	12 ♂3, 37 ♂2
25	335	133	64	129	1 ♂3, 63 ♂2
26	385	153	86	148	62 ♂2, 24 ♂1
27	430	171	108	165	57 ♂2, 51 ♂1
28	462	184	136	178	42 ♂2, 94 ♂1
29	492	196	163	189	26 ♂2, 137 ♂1
30	520	207	198	199	1 ♂2, 197 ♂1
July 1	544	216	240	209	209 ♂1, 31 ♂0
2	563	225	272	217	217 ♂1, 55 ♂0
3	573	228	320	220	220 ♂1, 100 ♂0
4	580	231	352	222	222 ♂1, 130 ♂0
5	582	232	374	223	224 ♂1, 150 ♂0
6	583	233	379	224	231 ♂1, 148 ♂0
7	582	232	374	223	243 ♂1, 131 ♂0
8	580	231	352	222	262 ♂1, 90 ♂0
9	573	228	320	220	284 ♂1, 36 ♂0
Total	9056	Total 3600			
10	563	225	272	217	
11	544	216	240	209	
12	520	207	198	200	
13	492	196	163	184	
14	462	184	136	178	
15	430	171	108	165	
16	385	153	86	148	

parasitism is inevitable if the full complement of parasite eggs is laid, and that right up to the end of June the daily production of host eggs is less than that of parasite eggs. Later, in the first half of July, as the rate of host production rises to a maximum, superparasitism ceases, and a considerable number of the hosts remain unattacked. Later still, from 12 July onwards, the rate of parasite production again exceeds that of the hosts, but superparasitism does not reappear to anything like the same degree. This is because it takes at least a week for the host larva to emerge, so that some of the unparasitized hosts laid on 5 July and after receive a proportion of the surplus parasite attacks on and after 12 July. As a result, the sample of 3910 hosts in which we are interested receives more than its quota of 3600 parasites. To correct this, a slight proportional reduction of all the parasite numbers has to be made, as in the fifth column of the table, so that by the time the emergence

has taken place of all the host eggs laid not later than 9 July, not more than 3600 parasites have been distributed among them.

In the calculation of the arrangement of the parasite eggs, it is assumed that when no unparasitized hosts are available, the host which has been attacked only once will be preferred to that which has been twice attacked, the host with two parasites to that which contains three, and generally, that the hosts with the lowest number of parasites are always the most acceptable. The results are detailed in Table IV where the contraction *hn* denotes a host with *n* parasites, and are summarized in column A of Table VIII for comparison with the field data. The correspondence is not very close, but it is enough to show that host shortage is quite capable of producing a distribution which, judged by itself, might imply rather poor powers of discrimination on the part of the ovipositing parasites.

Two modifications of the present hypothesis suggest themselves. It was assumed that although the parasites could select healthy hosts with complete certainty, they would nevertheless continue ovipositing however heavy the superparasitism. One would expect that with superior discriminative faculties the egg-laying activities would to some extent be curtailed, especially under circumstances such as those of the first few days of the oviposition period. But if the daily numbers of parasite eggs are reduced during the time when hosts are scarce, they will have to be correspondingly increased later on, in order that the full number of 3600 parasites may be accounted for, and this will bring about a decrease in the number of superparasites and an increase in the number of hosts with one parasite, i.e. in the total number of hosts parasitized. The final result will thus be even more unlike the observed distribution. The other suggestion is that although the female parasites are capable of searching out all the available healthy hosts when necessary, they do not distinguish between heavily and lightly parasitized hosts, and therefore if forced to superparasitize, do so indiscriminately. This obviously makes no difference to the total number of hosts attacked, and as shown in column B of Table VIII, gives quite a good distribution in the cases of the hosts with the higher numbers of parasites.

As a contrast we will examine the case in which the parasites are assumed to distribute their progeny at random among the hosts. The time interval between the laying and hatching of the host egg is now of more importance. This has been recorded as 7–10 days, depending in all probability on the temperature. For convenience an average of 8 days will be used. In Table V the second and third columns give the numbers of host and of parasite eggs produced every day. Since the female parasite does not distinguish between the healthy and parasitized hosts there can be no question of her exercising any restraint because of superparasitism. Therefore we have that on 17 June, 2 hosts receive 20 parasites. On 18 June there are 5 new hosts making altogether 7, among which are distributed 26 parasites. On 19 June, 33 parasites are distributed among a total of 17 hosts, and so on up to 24 June when

93 parasites are distributed at random among 172 hosts. On 25 June there are 64 new hosts, but by this time, 8 days having passed, the host eggs laid on 17 June have hatched, so that the number of hosts now available is 234 and among these 108 parasite eggs are distributed. Similarly, by 26 June the hosts of 18 June have hatched, and the parasite eggs are shared among the hosts of 19–26 June. This process must be continued until the host eggs laid on 9 June have hatched, i.e. until 16 June. It will be recalled that it was estimated that host eggs laid after 9 July do not reach the base of the stem by the time the wheat is cut. With the parasite eggs, on the other hand, not

Table V

Date	No. of host eggs laid	No. of parasite eggs laid	No. of parasites received by host	Parasite distribution
June 17	2	20	39	Say 1 *h*24, 1 *h*15
18	5	26	51	1 *h*12, 1 *h*11, 1 *h*10, 2 *h*9
19	10	33	70	1 *h*9, 2 *h*8, 4 *h*7, 2 *h*6, 1 *h*5
20	15	42	82	1 *h*9, 1 *h*8, 2 *h*7, 3 *h*6, 4 *h*5, 2 *h*4, 1 *h*3, 1 *h*2
21	22	53	97	1 *h*8, 2 *h*7, 3 *h*6, 4 *h*5, 5 *h*4, 4 *h*3, 2 *h*2, 1 *h*1
22	30	65	110	2 *h*7, 3 *h*6, 4 *h*5, 6 *h*4, 7 *h*3, 5 *h*2, 3 *h*1
23	39	79	120	1 *h*7, 2 *h*6, 4 *h*5, 7 *h*4, 10 *h*3, 9 *h*2, 5 *h*1, 1 *h*0
24	49	93	128	1 *h*6, 5 *h*5, 8 *h*4, 10 *h*3, 13 *h*2, 9 *h*1, 3 *h*0
25	64	108	142	1 *h*6, 4 *h*5, 7 *h*4, 13 *h*3, 17 *h*2, 15 *h*1, 7 *h*0
26	86	125	160	3 *h*5, 7 *h*4, 15 *h*3, 23 *h*2, 26 *h*1, 12 *h*0
27	108	139	171	2 *h*5, 7 *h*4, 15 *h*3, 26 *h*2, 36 *h*1, 22 *h*0
28	136	150	183	1 *h*5, 6 *h*4, 14 *h*3, 32 *h*2, 48 *h*1, 35 *h*0
29	163	159	187	1 *h*5, 4 *h*4, 13 *h*3, 33 *h*2, 61 *h*1, 51 *h*0
30	198	168	195	3 *h*4, 12 *h*3, 37 *h*2, 73 *h*1, 73 *h*0
July 1	240	176	206	3 *h*4, 11 *h*3, 37 *h*2, 87 *h*1, 102 *h*0
2	272	182	206	2 *h*4, 9 *h*3, 37 *h*2, 97 *h*1, 127 *h*0
3	320	186	217	1 *h*4, 9 *h*3, 38 *h*2, 110 *h*1, 162 *h*0
4	352	188	219	1 *h*4, 8 *h*3, 37 *h*2, 117 *h*1, 189 *h*0
5	374	188	219	1 *h*4, 7 *h*3, 36 *h*2, 122 *h*1, 208 *h*0
6	379	189	213	1 *h*4, 6 *h*3, 35 *h*2, 121 *h*1, 216 *h*0
7	374	188	207	1 *h*4, 6 *h*3, 33 *h*2, 119 *h*1, 215 *h*0
8	352	188	196	1 *h*4, 6 *h*3, 31 *h*2, 112 *h*1, 202 *h*0
9	320	186	182	1 *h*4, 6 *h*3, 28 *h*2, 104 *h*1, 181 *h*0
			Total 3600	
10	272	182		
11	240	176		
12	198	168		
13	163	159		
14	136	150		
15	108	139		
16	86	125		

only those laid before 9 July, but in addition a considerable number of those produced between 9 and 16 July will be present in the stubble. And it is for this reason that in Table V the daily numbers of parasite ovipositions have to be so much reduced in comparison with the corresponding numbers in Table IV.

The most convenient formula for calculating how many hosts receive 1, 2, 3, etc., parasites in a random distribution is the one described by Stoy (1932). It gives the probable number of hosts that will receive p parasites if x parasites are distributed among N hosts, provided that all of the x parasites have equal chances of being placed in any of the N hosts. Selecting a particular host, the

probability that it receives any given parasite is $1/N$, and the probability that it does not receive this parasite, i.e. that the parasite goes into any of the other $N-1$ hosts is $(N-1)/N$. The probability that a particular host receives a set of p chosen parasites is the product of the possibilities that it receives those parasites and that it does not receive the remaining $x-p$ parasites, all these probabilities being supposed to be independent. The expression for this probability is therefore

$$\left(\frac{1}{N}\right)^p \left(\frac{N-1}{N}\right)^{x-p}.$$

But out of x parasites a group of p can be chosen in ${}_xC_p$ ways, where

$${}_xC_p = \frac{x\,(x-1)\,(x-2)\,\ldots\,(x-p+1)}{p\,(p-1)\,(p-2)\,\ldots\,1},$$

so that the probability that the host receives any p parasites is

$${}_xC_p \left(\frac{1}{N}\right)^p \left(\frac{N-1}{N}\right)^{x-p},$$

and since there are N hosts altogether the probable number of these to receive p parasites where x parasites are distributed among them at random is

$$N\,{}_xC_p \left(\frac{1}{N}\right)^p \left(\frac{N-1}{N}\right)^{x-p}.$$

When N and x are known the required numbers are obtained by substituting the values 0, 1, 2, 3, etc., for p.

In order to utilize this formula, the next step is to find the total number of parasites received by each group of hosts. Since 17 June is the first day in which host eggs appear, they must receive all of the 20 parasite eggs laid on that date. On 18 June there are 5 new hosts making 7 in all, but since there is no preference for them in virtue of their not being parasitized, their expectation is only $\frac{5}{7}$ of the 26 parasites, the remaining $\frac{2}{7}$ being added to the 20 already present in the other 2 hosts. In addition, in exactly the same way, these 2 hosts receive on 19 June $\frac{2}{17} \times 33$ parasites. On 20 June $\frac{2}{32} \times 42$ parasites, on 21 June $\frac{2}{54} \times 53$ parasites, and so on for 8 days up to 24 June, when they receive $\frac{2}{172} \times 93$ parasites, making a total of 39 parasites. Again in the same way, the group of 5 hosts of 18 June receives in addition to $\frac{5}{7} \times 26$ parasites on 18 June, $\frac{5}{17} \times 33$ on 19 June, $\frac{5}{32} \times 42$ on 20 June, etc., and finally $\frac{5}{234} \times 108$ on 25 June, altogether 51 parasites. In Table V the fourth column shows the number of parasites worked out in this method to be the share of each group of hosts, the total number of parasites distributed in 3910 hosts now being the requisite 3600. This division of the parasites in proportion to the numbers of the host groups which are present on each day in turn is adopted for want of a better way of overcoming the problem of the variation of host population. While not strictly in accordance with the laws of random distribution, it does not introduce any appreciable error. The parasite distribution in each group of hosts is given in the final column of Table V and the sum-

mation of these results in Table VIII, column C. Comparison with the field data and with column B, shows that quite definitely the progeny of *Collyria* are not distributed at random among the hosts, and also that, on the whole, column B more closely resembles the facts than does column C. This can be taken to indicate a considerable degree of discrimination on the part of the ovipositing females.

Having shown that the observed distribution of *Collyria* eggs is in agreement with the hypothesis that the females exercise discrimination in some degree at least when they oviposit, we can now proceed to consider by what possible means a parasite may be led to accept one host and refuse another. The *Cephus* eggs lie inside the lumen of the wheat-stalk, and are not exposed to direct examination by parasites. Confining our attention in the meantime, to reactions in terms of senses which we as humans can comprehend, we have the possibility that when a *Collyria* attacks a *Cephus* egg, the pressure of her body against the surface of the stalk during the effort of discharging the egg, causes a deposition of a trace of secretion in the same way that we leave finger-prints on everything we touch. This residue would have an odour characteristic of the species, and any other *Collyria* coming along shortly after the first had left would have evidence that as regards this particular host she had been forestalled. After a time the odour or taste would naturally become less pronounced and it is possible that it might become completely ineffective as a deterrent to further oviposition, so that the next *Collyria* to investigate it finds what according to her reactions is a normal, healthy host. Thus although the truth of this idea has still to be proved observationally, from the theoretical aspect it is valid because it is in agreement with the evidence that *Collyria*'s recognition of parasitized hosts is only partial.

To start with a simple case, it will be assumed that the result of any act of parasite oviposition is a smell which for 1 day inhibits further attack on that particular host. In other words, unless at a time of host shortage, a host does not receive more than one parasite egg per day. The calculation of the parasite distribution is quite straightforward. It will be seen from the fifth column of Table VI that the total numbers of hosts received by the successive groups of hosts are exactly the same as for random distribution, and indeed up to that point the method of calculation is the same. An interval of 8 days elapses between the laying of host eggs and the emergence of the larvae, so that on any day the host population consists of the eggs laid on that day together with those laid on the 7 previous days. The parasite eggs are divided among the eight groups in the proportion of the sizes of the groups. Column 4 of Table VI details the numbers of eggs received by the host groups on each of the 8 days of the egg stage. As a typical example we will examine the distribution of parasites in the group of 64 host eggs laid on 25 June. On that day there are altogether 234 host eggs; therefore of the 108 parasite attacks, these 64 particular hosts receive $\frac{64}{234} \times 108 = 29$; and so that at the end of the day there are 29 of them with 1 parasite each and 35 unparasitized. By the following day

the odour resulting from the contact of the parasite is assumed to have diminished to an extent such that the 29 parasitized hosts are indistinguishable from the remaining healthy ones. On 26 June the 64 hosts receive a share of parasite eggs amounting to 26, and since the females cannot knowingly avoid the 29 parasitized hosts, the expected division of the new eggs among the parasitized and healthy hosts is in the ratio 29 : 35 which is to the nearest whole number 12 : 14. Thus the 29 hosts containing 1 parasite each become 12 *h*2 plus 17 *h*1, while the 35 unparasitized hosts become 14 *h*1 plus 21 *h*0, altogether 12 *h*2, 31 *h*1, 21 *h*0. Similarly by 27 June the 64 hosts are once

Table VI

Date	No. of new hosts	No. of parasite eggs Laid	No. of parasite eggs received on 1st day	2nd day	3rd day	4th day	5th day	6th day	7th day	8th day	Total	Parasite distribution
June 17	2	20	20	7	4	3	2	1	1	1	39	1 *h*24, 1 *h*15
18	5	26	19	9	6	5	4	3	3	2	51	1 *h*12, 1 *h*11, 1 *h*10, 2 *h*9
19	10	33	20	13	10	8	6	5	5	3	70	4 *h*8, 3 *h*7, 2 *h*6, 1 *h*5
20	15	42	20	15	12	10	8	7	6	4	82	3 *h*7, 5 *h*6, 4 *h*5, 2 *h*4, 1 *h*3
21	22	53	21	17	14	12	10	9	8	6	97	1 *h*7, 3 *h*6, 6 *h*5, 7 *h*4, 4 *h*3, 1 *h*2
22	30	65	23	19	16	14	12	10	9	7	110	2 *h*6, 6 *h*5, 9 *h*4, 7 *h*3, 5 *h*2, 1 *h*1
23	39	79	26	21	18	15	13	10	9	8	120	2 *h*6, 3 *h*5, 8 *h*4, 13 *h*3, 9 *h*2, 4 *h*1
24	49	93	27	23	19	17	14	12	9	7	128	3 *h*5, 9 *h*4, 13 *h*3, 14 *h*2, 10 *h*1
25	64	108	29	26	22	18	15	13	10	9	142	3 *h*5, 6 *h*4, 17 *h*3, 19 *h*2, 14 *h*1, 5 *h*0
26	86	125	35	29	24	20	17	14	11	10	160	2 *h*5, 5 *h*4, 16 *h*3, 28 *h*2, 26 *h*1, 9 *h*0
27	108	139	36	31	25	22	19	15	12	11	171	6 *h*4, 15 *h*3, 32 *h*2, 38 *h*1, 17 *h*0
28	136	150	38	32	27	23	20	17	14	12	183	4 *h*4, 14 *h*3, 37 *h*2, 51 *h*1, 30 *h*0
29	163	159	39	32	28	24	20	17	15	12	187	3 *h*4, 12 *h*3, 37 *h*2, 65 *h*1, 46 *h*0
30	198	168	40	34	28	24	21	18	16	14	195	2 *h*4, 10 *h*3, 39 *h*2, 79 *h*1, 68 *h*0
July 1	240	176	41	35	30	25	22	20	18	15	206	1 *h*4, 11 *h*3, 37 *h*2, 95 *h*1, 96 *h*0
2	272	182	40	34	29	25	23	20	19	16	206	8 *h*3, 39 *h*2, 104 *h*1, 121 *h*0
3	320	186	39	34	29	27	24	23	22	19	217	8 *h*3, 38 *h*2, 117 *h*1, 157 *h*0
4	352	188	37	32	29	27	25	24	24	21	219	7 *h*3, 37 *h*2, 124 *h*1, 184 *h*0
5	374	188	35	31	28	27	26	25	25	22	219	7 *h*3, 33 *h*2, 132 *h*1, 202 *h*0
6	379	189	31	29	27	26	25	25	25	25	213	5 *h*3, 35 *h*2, 128 *h*1, 211 *h*0
7	374	188	28	27	26	25	25	25	25	26	207	5 *h*3, 32 *h*2, 128 *h*1, 209 *h*0
8	352	188	25	24	24	23	24	25	25	26	196	5 *h*3, 30 *h*2, 121 *h*1, 196 *h*0
9	320	186	22	21	21	21	22	24	25	26	182	5 *h*3, 28 *h*2, 111 *h*1, 176 *h*0

more all alike to the attacking parasites, and their share of the 139 parasite eggs, amounting to 22, has an expected distribution in the ratio 12 : 31 : 21, which is roughly 4 : 11 : 7, making 4 *h*3, 8 *h*2; 11 *h*2, 20 *h*1; 7 *h*1, 14 *h*0; i.e. 4 *h*3, 19 *h*2, 27 *h*1, 14 *h*0. This procedure is continued for each day up to 2 July, when the expectation of parasitism in the 64 emerging host larvae is 3 with 5 parasites each, 6 with 4, 17 with 3, 19 with 2, 14 with only 1, and 5 unparasitized.

The summarized parasite distribution for the sample of 3910 hosts is given in column D of Table VIII. It is a slight improvement on random distribution, not only as regards the total number of hosts parasitized, but also in respect of the numbers of hosts containing more than three parasites. In working out this result, the parasites were assumed to be laying freely at the beginning in spite of the scarcity of hosts. If we say that under no circumstances can a host receive more than one egg in a day, the greatest number of parasites per host is 8, or at the outside 10, and we cannot account for the observed

case of 16 parasites in one *Cephus*. Besides, if the basis of the calculation is not more than 1 parasite per host per day, the numbers of hosts with 7 and 8 parasites are reduced, and the parasites which would have fallen to the lot of the most frequently attacked hosts instead cause an increase in the number of those with 2 or 3 parasites, so that altogether the modification is unsatisfactory.

The extent of discrimination observed in *Collyria* is considerably greater than that shown by the hypothetical parasite whose act of oviposition in a host safeguards that host from a further attack until the following day. It was found that if a parasitized host is assumed to be unacceptable for a period of 2 days after the first attack, the result is greatly improved, altogether 2501 hosts being parasitized. With an interval of 3 days, 2652 hosts are attacked, and with one of 4 days the total is 2824. The distribution given by the 3-day period does in fact bear a certain resemblance to that of *Collyria*, but for reasons which will be discussed later, the idea of such a prolonged interval was discarded.

Another possibility worth consideration is that when the parasite larva hatches within the host its movements may be detectable by adult parasites which come to examine the host. Larval movement may act as a safeguard against the introduction of more parasite eggs. There is no record of the extent of time between the laying and hatching of a parasite egg, but a *Cephus* egg containing a young *Collyria* larva has been observed (Salt, 1931, p. 511). In the present case the parasite distribution is worked out on the two assumptions: first, that normally a host is not attacked more than once in a day; secondly, that the parasite larva emerges 6 days after oviposition and its movements inside the host put a stop to all further attack. With regard to the latter hypothesis, the first larva to hatch determines the beginning of the host's permanent immunity, and further, if the host egg is not attacked on the first or second day of its existence in the stalk, larval movement will not play any part in limiting the number of parasites it can receive. The arithmetical method is essentially the same as that employed for the previous example, and for the calculation the daily numbers of parasite ovipositions are the same as those in Table VI. On any one day the parasite eggs are assumed to be distributed uniformly among all the hosts which are acceptable to the female parasites, that is to say among the unparasitized hosts and those containing parasite eggs, but not among those with parasite larvae, each group of host eggs receiving parasites in proportion to the number of its suitable members. Except for the numbers of hosts with 2 or 3 parasites, this distribution (see column E of Table VIII) is better than the one which resulted from the previous hypothesis.

To return to the concept that an act of oviposition leaves material evidence which can be detected by other females of the species, we have already seen that it is insufficient to assume an odour of which the effect is transient. Leaving aside, for the present, the possibility that the parasite can detect and

appreciate the significance of larval movements inside the host eggs, let us see how we can modify the application of a reaction to smell. It is quite within reason to suppose that if a parasite arrives at a host which only a short time before has received an egg from another parasite, the second individual will not oviposit unless there is nothing better in the vicinity. The rejection of the host may be because there is an actual knowledge of the egg already inside it, or it may be simply a reaction to something unfavourable. If a smell is a means of preventing superparasitism, the passing of time is likely to reduce its effectiveness, although it may not necessarily reduce it altogether. The first assumption was that on the day following an attack parasitized hosts are indistinguishable from healthy ones. But if the smell were still present in a slight degree, the parasitized hosts might be accepted by some parasites and refused by others with more acute senses. Again, the investigation of a healthy host is not always followed by oviposition, and we might suppose that whereas a female parasite would attack, say, 4 out of 5 of the healthy hosts she found, she would accept only 2 out of every 5 which had been attacked on the previous day or earlier, that is, which gave only a faint indication that other females had been at work there. Hosts which had only just been attacked would of course all be refused. Of a parasite behaving in the way which has just been outlined, it can be said that with every host she finds the likelihood of her attacking a healthy one is twice as great as that of her attacking one which is parasitized. The ratio in which the parasite eggs are divided depends on the relative numbers of the two kinds of hosts. Equal amounts of healthy and parasitized hosts means a 2 : 1 division of the parasite eggs. In general, the number of each kind that the parasite accepts must depend on the number that she finds. Thus suppose a population consisted of 40 healthy and 20 parasitized hosts. If a parasite found 30 of them in the course of a day, the expectation is that those 30 would comprise 20 healthy and 10 parasitized hosts. By accepting 4 out of 5 healthy hosts the parasite would attack 16 of them, and by accepting 2 out of 5 of the parasitized hosts she would superparasitize only 4, making the distribution ratio 4 : 1. The rule is: to find the ratio in which to divide a group of parasites among the healthy and parasitized hosts of a population, the ratio between the numbers of the two types of hosts is multiplied by the factor for the parasites' preference.

In the present problem the parasite distribution was calculated with various values, 2, 3, 4, etc., as a measure for the parasites' preference for healthy hosts. The total numbers of healthy and parasitized hosts of a population are found for each day. The parasite eggs are first of all divided according to the process described above to allow for the females being less ready to accept parasitized hosts. The parasites allotted to each kind of host are then subdivided proportionately among the several host groups in the way which has been detailed earlier. Naturally, the greater the preference for healthy hosts that the parasites are assumed to have, the less will be the number of superparasites and the greater the total number of hosts infested, and it was

found that when the preference factor is rated as high as 4, the amount of superparasitism is no greater than the actual finding of *Cephus* (column F, Table VIII). In addition, it can be seen that the hypothetical arrangement is, term by term, a fairly good match for the distribution in the field material. The greatest errors are in the numbers of hosts with 2 and 4 parasites.

The next column, G, of Table VIII, shows the combined effect of the larval movement and smell ideas. The female parasites are supposed to reject hosts which have obvious signs of recent attack; to accept those on which, through the passing of time the evidence of parasitism has diminished, but only one-fourth as readily as they accept healthy hosts; and finally, to reject hosts in which parasite larvae can be detected moving about. There is very little difference between this and the previous result. Such as there is, is not an improvement.

Continuing with the question of the parasites' relative reluctance to accept certain parasitized hosts, we have seen that it is possible to find a value for what may be termed the "factor of preference" such that in the hypothetical distribution the proportion of superparasites is the same as that in the parasitism of *Cephus* by *Collyria*. We have also seen that for this particular value, 4, the arrangement of parasites obtained arithmetically shows a considerable correspondence with that in the *Cephus* material. The assumption was that independently of the ratio between healthy and parasitized hosts, the examination of a healthy host is followed by oviposition four times as frequently as the examination of a parasitized host is followed by oviposition. Now consider the following possibilities. Suppose parasites to be searching in a host population which is already heavily parasitized, say 95 per cent. And again, suppose them to be at work in another collection of hosts where 95 per cent of them are healthy. In the former case they will only now and then come across an unparasitized host. In the latter, practically every host encountered will be healthy, and it seems quite reasonable to suppose that in such circumstances, when a parasite finds a host about which there is even a faint suggestion of the previous visit of another of its kind, she can afford to move on to the next host which will probably not have been parasitized before. On the other hand, if healthy hosts are very seldom found as in the first instance, the parasites will surely be less likely to keep on rejecting those the state of which, according to their sensory reactions, is doubtful. Would it not be better to assume that the factor of preference for healthy hosts, instead of being a constant, is some function of the ratio between the numbers of healthy and parasitized hosts? The simplest relationship is that it is proportional to the ratio. This can be written

$$F = K\frac{U}{P},$$

where K is a constant, and U and P are the numbers of healthy and parasitized hosts respectively. U and P are, of course, themselves functions of the host and parasite activities and depend ultimately on the relative times and

rates of emergence of the two interacting species. The best value for K must be found by trial. Again 4 gave a successful result. In practice, in the estimation of F it is convenient to assume its value to be constant for any one day. For each day in turn the numbers of parasitized and unparasitized hosts are counted up, the value of $K(U/P)$ found and then the parasite eggs distributed according to that particular F. To illustrate, it can be seen from Table VII

Table VII

Date	No. of host eggs laid	No. of parasite ovipositions	Parasite distribution
June 17	2	20	1 *h*18, 1 *h*14
18	5	27	1 *h*11, 2 *h*9, 2 *h*8
19	10	34	1 *h*8, 4 *h*7, 4 *h*6, 1 *h*5
20	15	44	1 *h*7, 4 *h*6, 6 *h*5, 1 *h*4, 3 *h*3
21	22	55	1 *h*6, 7 *h*5, 7 *h*4, 6 *h*3, 1 *h*2
22	30	67	4 *h*5, 11 *h*4, 10 *h*3, 5 *h*2
23	39	81	1 *h*5, 11 *h*4, 11 *h*3, 10 *h*2, 6 *h*1
24	49	96	7 *h*4, 13 *h*3, 17 *h*2, 12 *h*1
25	64	112	6 *h*4, 10 *h*3, 25 *h*2, 22 *h*1, 1 *h*0
26	86	128	3 *h*4, 11 *h*3, 29 *h*2, 41 *h*1, 2 *h*0
27	108	143	1 *h*4, 12 *h*3, 29 *h*2, 64 *h*1, 2 *h*0
28	136	154	9 *h*3, 29 *h*2, 90 *h*1, 8 *h*0
29	163	164	6 *h*3, 29 *h*2, 111 *h*1, 17 *h*0
30	198	173	3 *h*3, 28 *h*2, 135 *h*1, 32 *h*0
July 1	240	181	1 *h*3, 24 *h*2, 162 *h*1, 53 *h*0
2	272	188	21 *h*2, 176 *h*1, 75 *h*0
3	320	191	19 *h*2, 199 *h*1, 102 *h*0
4	352	193	14 *h*2, 209 *h*1, 129 *h*0
5	374	194	13 *h*2, 214 *h*1, 147 *h*0
6	379	195	12 *h*2, 211 *h*1, 156 *h*0
7	374	194	12 *h*2, 203 *h*1, 159 *h*0
8	352	193	10 *h*2, 193 *h*1, 149 *h*0
9	320	191	11 *h*2, 176 *h*1, 133 *h*0

that, assuming there is an interval of 8 days between the laying and hatching of a host egg, there are 413 host eggs in existence on 27 June. Of these it happens that 150 are healthy and 263 contain parasites, so that

$$F = K\frac{U}{P}$$
$$= \frac{4 \times 150}{263}$$
$$= 2{\cdot}28$$

and, therefore, the 143 parasite eggs are distributed among 150 healthy and 263 parasitized hosts in the ratio

$$150 \times 2{\cdot}28 : 263$$

or

$$342 : 263$$

which is 81 in the healthy hosts and 62 superparasites. In contrast, later in the season, on 8 July for example, there are 2663 hosts of which 1711 are healthy while 952 contain parasites, giving

$$F = \frac{4 \times 1711}{952}$$
$$= 7{\cdot}19$$

and so the 193 parasite eggs are divided between the healthy and parasitized hosts in the ratio

$$1711 \times 7{\cdot}19 : 952$$

or

$$12302 : 952$$

which is 179 parasites in healthy hosts and only 14 superparasites. It should be noted that on this, an occasion when unparasitized hosts are plentiful, the factor for the parasites' preference for unparasitized hosts has increased to more than three times its value on 27 June.

The addition of the separate results in the final column of Table VII shows that the 2910 hosts receive 3642 parasites. The required total of 3600 is obtained by finding the numbers of parasites in each of the hosts-groups—hosts with 1 parasite each, with 2 parasites each, and so on—and reducing each of these numbers by $\frac{1}{87}$. The resulting parasite distribution is given in column H of Table VIII. This particular combination of hypotheses is found to produce a parasite distribution similar to what has been found in *Cephus*, and in so far as it has done that, it forms an adequate description of the reactions of female *Collyria* to their hosts.

Table VIII

No. of parasites in a host	Observed no. of hosts	Calculated no. of hosts							
		A	B	C	D	E	F	G	H
0	1198	871	871	1806	1727	1648	1204	1173	1191
1	2195	2615	2764	1266	1348	1422	2124	2151	2206
2	332	329	151	510	530	554	425	440	333
3	98	75	60	182	183	187	91	86	94
4	49	13	30	74	62	56	31	33	46
5	18	2	13	33	28	20	17	13	19
6	7	3	9	15	14	11	7	5	8
7	4	0	5	11	7	4	4	3	5
8	5	0	2	4	4	2	2	2	3
9	2	0	1	4	2	2	1	1	2
10	0	0	1	1	1	1	1	1	0
11	1	2	1	1	1	1	1	0	1
12	0	—	0	1	1	0	1	1	0
13	0	—	0	0	0	0	0	0	0
14	0	—	0	0	0	0	0	0	1
15	0	—	0	1	1	0	0	0	0
16	1	—	1	0	0	0	1	1	0
17	—	—	0	0	0	1	—	—	1
18	—	—	0	0	0	0	—	—	—
19	—	—	1	(24) 1	(24) 1	1	—	—	—
No. of hosts parasitized	2712	3039	3039	2104	2183	2262	2706	2737	2719
No. of super-parasites	882	561	561	1496	1417	1338	894	863	881

VIII. Discussion

In the foregoing part of the paper it has been shown how it is possible, on the basis of certain assumptions, to build up a hypothetical parasite distribution corresponding to that of *Collyria* in its host *Cephus*. The assumptions are of two types: primary, those which are related to the longevity of the insects and which serve to provide a graphical representation of their relative

activity during the oviposition period; and secondary, those dealing with the parasite's reactions to the host, which give the expected distribution of parasite progeny for any particular conditions of host and parasite activity. As it has been pointed out, the choice of the number of days for the expectation of life of *Collyria* and *Cephus* is at best a not too unlikely guess. After that the hypotheses made regarding *Collyria*'s acceptance of a host are retained or discarded according to whether the result obtained from them is good or bad, but it must be remembered that the real error may have been introduced in the earlier stage. The adults of *Collyria* continue to emerge over a period of a month, so that if the dates on which it was first seen and last seen in a season were recorded the interval between them, less one month, would represent the length of adult life. In the same way, the life of *Cephus* might be estimated. But since the first few emergents and the last survivors would probably pass unnoticed, the estimates would tend to be too low. In captivity, the insects might or might not suffer from the environment; it might not be easy to judge whether they were enjoying normal health, and in any case under these circumstances no allowance could be made for predators. The selection of 25 days' life for *Collyria* and of 6 days for *Cephus* is certainly within reason, for these are the values which, when used in conjunction with such facts as have actually been observed about the emergence of the two species, give a parasite population attaining its maximum just when the hosts are most plentiful, yet not outliving the time that they continue to be available—a point of importance since in England at least there is no alternative host for *Collyria*. In short, the choice was made to give the most advantageous arrangement of the parasite in relation to its host.

A striking feature of the infestation of *Cephus* by *Collyria* is that although the numbers of parasites in certain hosts can be very high considering that only one survives, yet the proportion of these highly parasitized hosts is small —out of nearly 4000 *Cephus* only 20 contain 6 or more parasites. This suggests that the intense superparasitism occurs at a time when the parasites are very anxious to oviposit in spite of the scarcity of hosts; that is to say during the first few days of the *Cephus* egg-laying period. The *Collyria* have already emerged in considerable numbers. When there are only a few hosts they must be more difficult to find, but if the daily average number of ovipositions by a *Collyria* is not a large number, say 10, and there are on an average 4 hours a day suitable for oviposition, there is plenty of time during that period in which to carry out an extensive search for hosts. Again there is the fact that some of the parasites have to wait several days with no opportunity at all of ovipositing, so that there may be to some extent an accumulation of ripe eggs in the ovary. This might result in an increased desire to get rid of eggs, and hence in a more energetic search for hosts and in a continuation of egg laying in spite of the supply of healthy host material being soon exhausted. This idea is in part supported by the work of Mr D. C. Lloyd on *Ooencyrtus* (*Schedius*) *kuvanae* How., a chalcid egg parasite of *Porthetria dispar*, wherein he found

that parasites which were prohibited from ovipositing for some days after their emergence, laid numbers of eggs much higher than the normal daily average. It is true that a certain degree of restraint appeared to be exercised by females when offered previously parasitized material (Lloyd, 1935), but as Ullyett (1936) points out, a parasite confronted with a number of hosts, all more or less close together in a dish, is not at all in the same position as one in the field, where, if the population is small, she has to perform a considerable amount of searching between the finding of one host and another. The present assumption for *Collyria* is that the greater difficulty of finding hosts at the beginning of the season, and the reluctance to accept hosts which are obviously parasitized, is compensated by the increased desire to oviposit and that the normal rate of oviposition is maintained.

In his investigation of host selection by *Microplectron fuscipennis* Zett., Ullyett (1936) found that there was no apparent discrimination between healthy hosts and those containing parasite eggs, that when the female parasites were offered both types to choose from, they were accepted with equal readiness. On the other hand, when the parasites in the hosts were mature larvae there was a decided preference for healthy hosts when *Microplectron* was allowed a choice between the two. From this it was thought that vibrations set up by the movements of the parasite larvae might be detected by the female as she examined the hosts with her antennae. That this may be true in the case of *Collyria* also is quite possible. At the same time it must be remembered that the ovipositor is the only part of this insect that is ever in direct contact with its host, and that the antennal examination is confined to the outside of the wheat-stem, or at the nearest, to the incision left by the *Cephus*'s ovipositor. The inference from these considerations is that for *Collyria* the movements of larvae within the hosts can be of only very slight help in indicating which hosts are already parasitized, particularly as a *Cephus* egg can never contain other than very young parasite larvae. This is borne out by the mathematical evidence. In columns D and E of the result table are two distributions based on the hypothesis that a host which has just been parasitized has a certain period of immunity from further attack. The second, which includes the extra postulate that the host's immunity becomes absolute when the parasite egg hatches, shows an increase of only 79 on the number of hosts parasitized in the first. Still more striking is the case when larval movement is taken to be the only means by which the parasites can recognize that hosts are parasitized. The series is not worked out in complete detail, but on a rough estimate the writer finds that compared with the distribution which is entirely at random (column C) there is an increase of no more than 25 in the total number of hosts attacked. The insignificance of this amount is realized when it is pointed out that the difference between the numbers of hosts attacked in the real distribution of *Collyria* and in the theoretical random distribution is 608.

The stimulus responsible for the rejection of a parasitized host may be

chemical, and may be external to, or within, the host. In the latter case the chemo-receptor must be located on the ovipositor and it would be expected that the examination of a host would in many cases be followed by an insertion of the ovipositor which would *not* result in the laying of an egg. Observations of the reactions of *Ooencyrtus* females to parasitized gipsy moth eggs showed Mr D. C. Lloyd that this did not happen unless the object was to feed. The idea of an external chemical stimulus was brought forward by Salt & Laing (1935) who observed that with *Trichogramma evanescens* the females were able to distinguish between clean hosts and those with which other females of their species had been in contact. They suggested that with *Collyria* there may be chemical traces on the surface of the wheat-stalks, which indicate to the parasites that another of the same species has already been there. The detection of these traces may employ tactile or olfactory organs or both. An odour implies something volatile and therefore lasting only for a time. An organic residue would tend to dry up or might be partially rubbed off the stem, thus becoming through time less obvious to organs of touch. If the substance were entirely volatile it could be expected to be effective as long as the evaporation continued. With its final disappearance there would no longer be any indication that the host was parasitized. On this assumption it is necessary for the odour to continue for at least 3 days if superparasitism in the theoretical distribution is not to exceed that by *Collyria*. It is, however, much more likely that any trace of secretion left after the contact of a female's body in oviposition is only partially volatile. The smell, readily detected immediately after the host had been attacked, would diminish, but might still be faintly perceptible if the residue were touched. The evidence which was at first clearly indicative of the parasitized state of the host would begin to admit of some doubt. This was the basis of the theory that the period of the host's greatest immunity is the remainder of the day on which it is attacked, and since at least 12 hours must elapse between the cessation of the parasites' activities on one day and the recommencement of them on the next, it was assumed that by the second day the warning stimulus has become reduced to a partially effective state. If we assume that the refusal or acceptance of a host by a parasite depends on the presence or complete absence of traces left by an earlier parasite, it is not logical to suppose that such a purely mechanical reaction will break down and allow superparasitism when there is a shortage of hosts. But if we say that a parasite will sometimes accept a host which bears some indication of a previous attack even when healthy hosts are available, the difference between repeated superparasitism and discrimination is seen to resolve itself into a question of the degree of the ease with which healthy hosts can be found. One mathematical interpretation of this is that the probability that a parasitized host will be rejected depends on the relative frequency of healthy and parasitized hosts. This was the conception which produced arithmetically the counterpart of the distribution of offspring actually observed in *Collyria*, and it implies that when the parasites are ovipositing, they show an

ability to adjust themselves to the variations in the situation as a whole rather than an entirely automatic reaction to each host encountered.

Arising from this attempt to employ analytical methods for the investigation of host selection, there is the discovery that the variation in the relative size of the host and parasite population can have a very marked influence on the amount of superparasitism. In addition, the weather conditions, and possibly also the insects' feeding habits, will play their part. Consequently there are certain points worth observing if any further field work should be undertaken to verify the theories of *Collyria*'s reactions. Firstly, the weather conditions should be recorded for the season when the adults are on the wing. To avoid confusion from unnecessary details a broad outline would be sufficient, indicating the prevailing wind, if any, and whether the rain were more excessive at one period than at another. In the field selected for observation, the distribution of charlock and *Heracleum*, the food plants of the host and parasite respectively, should be noted. Then at intervals from the cessation of parasite oviposition till the time when the grain is cut, samples should be taken from various marked points in the field. From these the following information is desirable: The number of hosts per unit area, showing variations according to the locality in the field; the stage of development of the *Cephus* larvae; the number of parasites per host. By noting the stages of host development, it would be possible to rearrange the results of the entire collection of samples in the order in which the hosts appeared as eggs, and so to obtain the real distribution of *Collyria*, which corresponds to those in the final columns of Tables IV–VII. At the same time it may be possible to find if there is any correlation between the spatial distribution of *Collyria*, the fact that *Heracleum* on which it feeds grows at the edge of the field, and the wind.

IX. Summary

1. An outline of the life history of *Cephus pygmaeus* Linnaeus is given.

2. The parasites of *Cephus* are listed and are discussed briefly in relation to the particular parasite *Collyria calcitrator* Gravenhorst.

3. It is shown that if the host larvae collected from wheat-stubble in autumn are used for the investigation of the extent of parasitism by *Collyria*, allowance must be made for the fact that the parasite *Pleurotropis benefica* Gahan is intrinsically inferior to *Collyria*, and that its cocoons must represent hosts left unparasitized by *Collyria*.

4. In summer the adults of *Collyria* emerge, on the whole, earlier than those of the host *Cephus*. This suggests that at the beginning of the season of oviposition there will be a scarcity of hosts in comparison with the numbers of parasites wishing to oviposit. The relative activity of host and parasite during the egg-laying period is worked out on hypotheses of the average length of life of the individuals, and is shown diagrammatically.

5. The *Cephus* larvae travel down the stem and hibernate at the base. When the wheat is cut, a proportion of the larvae and their parasites are removed with the straw. The way in which this may prevent the stubble material from giving a true indication of the degree of parasitism in the population as a whole is discussed.

6. On the basis that 3910 hosts receive 3600 parasites, various hypothetical distributions are worked out arithmetically in order to find which type of discrimination between healthy and parasitized hosts gives an arrangement of parasites most in agreement with what has been found for *Collyria* in *Cephus*. The most satisfactory result is that obtained when it is assumed that the probability of an already parasitized host being re-attacked varies with the proportion of parasitized hosts. It is also shown that a shortage of hosts at a time of parasite activity may cause a high degree of superparasitism, thus giving a false impression of the parasite's power of discrimination.

7. Suggestions for further field work are given.

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EAST COAST FEVER; ITS TRANSMISSION BY TICKS IN KENYA COLONY

HYALOMMA IMPRESSUM NEAR *PLANUM* P. SCH. AS A VECTOR

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A long time has elapsed since Lounsbury and Theiler in South Africa showed that *Theileria parva*, the causal organism of East Coast fever, was transmissible to cattle by certain tick species of the genus *Rhipicephalus*. Apart from the experiments carried out by Montgomery (1913–15), there appear to have been no further attempts to ascertain the vectors of this disease in other territories. We considered it desirable, therefore, to review the position with regard to East Coast fever and its transmission by tick species in Kenya, to repeat the South African experiments, and to extend our investigations to the ability of all common local ticks to transmit the disease. We have been able to prove experimentally that a species outside the genus *Rhipicephalus*, viz. *Hyalomma impressum* near *planum* P. Sch.,[1] is capable of conveying the disease from an infected to a susceptible animal.

Towards the end of 1902, Lounsbury (1903) first transmitted East Coast fever to susceptible cattle by feeding adults of *Rhipicephalus appendiculatus* that had engorged as nymphae on an infected animal in Rhodesia. Later (1904), he produced the disease by feeding adults transferred from a beast that had died from an attack of East Coast fever.

Subsequently, Lounsbury (1906) and Theiler (1905–7) proved in many experiments that the disease could be transmitted by nymphae that had moulted from larvae fed on an infected beast. They were also able to incriminate as vectors the ticks, *R. capensis*, *R. evertsi*, *R. nitens*[2], and *R. simus*, but experiments with *Boophilus decoloratus*, *Amblyomma hebraeum* and *Hyalomma aegyptium* gave negative results. Montgomery (1913), in Kenya, confirmed the transmission of East Coast fever with *Rhipicephalus appendiculatus*, but later (1915) failed to produce the disease with *R. evertsi* and *R. pulchellus*.

Both Theiler and Lounsbury concluded from their experiments that *R. appendiculatus* must be considered as the principal carrier of infection, and that the adult brown ticks (*R. appendiculatus*), which have been fed on sick animals as nymphae, must be considered as the main intermediate host.

[1] *Hyalomma* ticks in Kenya are not always typical of a species; and there appear to be transitional forms, or species in the making.

[2] = *R. appendiculatus*.

Experience in other territories, where East Coast fever exists, supports the view that *R. appendiculatus* is the usual common vector of the typical form of the disease; and it is the species which has been employed to produce the disease for experimental work on protective immunisation and other problems relating to *Theileria parva* in South Africa, Kenya Colony (Walker & Whitworth, 1929), England (Stockman in du Toit, 1931) and Algeria (Sergent *et al.* 1926). Field observations also seem to bear out the intimate relationship of *Rhipicephalus appendiculatus* and East Coast fever. Daubney & Hudson (1931) state that Kenya Colony can be divided into certain quite sharply delimited areas, in which East Coast fever is prevalent, and into other areas from which the disease is normally absent. In the former areas, *R. appendiculatus* is the tick commonly found on cattle and sheep, while in the latter it is absent.

More recently, peculiar forms of what may perhaps be East Coast fever have been met with in Kenya and in Uganda. In a communication to the Conference on the Co-ordination of Veterinary Research of the British East African Territories (1936), Daubney referred briefly to an often-repeated experience of the last four years in Kenya. He remarked: "In sporadic areas outbreaks of East Coast fever were often encountered in which it was extremely difficult to find Koch's bodies. Coincidently with the mortality from East Coast fever, many animals on the infected farms might contract a febrile condition simulating East Coast fever, which generally terminated in recovery. In most of these cases Koch's bodies could not be demonstrated." Mettam (1934, 1936) has drawn attention to a protozoan encephalitis associated with a *Theileria* apparently indistinguishable from *Theileria parva*. While he was unable to state that the parasite was identical with that of East Coast fever, he had observed that the disease—"turning sickness"—always occurred in cattle with a history of recovery from East Coast fever, or in cattle that had been drawn from enzootic East Coast fever areas. His attempts to transmit the disease artificially were unsuccessful, and his experiments with *R. appendiculatus* showed that it was impossible to transmit "turning sickness" by feeding this tick on calves recovered from East Coast fever. In addition, it would appear that such ticks were also free from the virus of East Coast fever since they failed to infect clean calves which, subsequently, proved susceptible on exposure to natural infection. It is interesting to note that in Kenya, where "turning sickness" is now popularly known under its native name, "Muthioko", a number of *R. appendiculatus* ticks collected as fully engorged nymphae from a case of this disease were allowed to moult to adults and then fed on an animal susceptible to East Coast fever. The test animal died of typical East Coast fever showing numerous Koch's bodies and small piroplasms in the lymphatic and the circulatory systems. Sections of cerebral cortex and medulla showed no lesions of "turning sickness". The incubation period of the disease, in this instance, was 26 days. Referring to this particular case, Daubney (vide *Report of the Chief Veterinary Research Officer for the year* 1934, Kenya Colony) stated that further experiments will be necessary to confirm

this finding, but it seems probable that the parasites of "turning sickness" and East Coast fever are identical.

In his preliminary communication, Mettam (1934) states: "The possibility exists that turning sickness may be due to a malignant strain of *Theileria parva*." In the second paper, Mettam & Carmichael (1936) point out: "The whole question of reinfection requires to be thoroughly investigated, particularly to test the view, widely held in Uganda, that cattle moved from one enzootic area to another relapse to East Coast fever. It is also necessary to know if different strains of *T. parva* exist which produce a solid group immunity but an unstable specific immunity. These are questions that are repeatedly asked in this part of Africa and to which at present no definite reply can be returned, especially in view of du Toit's (1931) recent pronouncement that there are wide variations in virulence within a species. In our opinion the solution of the nature of turning sickness may be elucidated during further investigations into this aspect of East Coast fever."

In view of the many difficulties encountered in the studies of East Coast fever, it seemed to us that a thorough and sustained investigation of the vectors and of the disease produced by different species of ticks might throw some light on the intricate problems associated with the disease and its control.

The ability of a tick to transmit the disease in nature is dependent upon several conditions, of which the life cycle of the species and the adaptation of the immature forms to their hosts are of significance. Conditions such as these may have an important bearing on the epidemiology of the disease, especially in areas where East Coast fever occurs sporadically.

Rhipicephalus appendiculatus is a three-host tick and it readily feeds in the larval, nymphal and adult stages on cattle. This species is commonly found where East Coast fever prevails. *R. capensis* and *R. simus* also are three-host ticks. Like Lounsbury (1906), we have found that the larvae of *R. capensis* are quite indifferent to the ox; we have failed, so far, to induce more than an extremely small number to feed on cattle; and it is not known what animal they usually feed on under natural conditions. Adults are frequently found on cattle in areas normally free from East Coast fever, and they are not very rare in other areas where the disease is common. The ox is also unsuitable as a host for the larvae of *R. simus*. Lounsbury (1906) found the dog to be a favourable host; and Daubney & Hudson (1934) fed numerous larvae on the field rat, *Arvicanthis abyssinicus*. Nymphae and adults, however, will feed readily on cattle. We have not often collected nymphae of *Rhipicephalus simus* from cattle, but adults are obtainable from domestic stock in all parts of the colony. In the case of *R. appendiculatus*, the larvae have every chance of taking up infection from an East Coast fever animal, and to transmit the disease as nymphae. The nymphae infest the ears of cattle in large numbers; they may become infected and convey the disease as adults. The chances of infection being carried from larvae to nymphae of *R. capensis* and *R. simus*

appear to be remote; and it is likely that only when the nymphae have fed on infected animals will the adults be able to transmit the disease.

R. evertsi is a two-host species; the larvae are usually found in the ears of cattle, where they moult to nymphae. The engorged nymphae drop off the host and moult to adults on the ground. In this instance again, the chances of transmitting infection occur only when the nymphae have sucked the blood containing parasites of East Coast fever, and have moulted to adults.

Our initial experiments on the transmission of East Coast fever have confirmed the results of other workers; and as we have already stated, *Hyalomma impressum* near *planum* P. Sch. is added to the list of proved vectors.

MATERIAL

The ticks used in our experiments were reared in the laboratory. Specimens originally collected in the field were fed on hares, rats, guinea-pigs, sheep and on cattle purchased from farms known to be free from East Coast fever. Several generations of the ticks were raised; and the different batches of larvae, nymphae and adults were tested at each stage. In the case of the beast suffering from "turning sickness", the ticks attached to the animal were allowed to engorge. These were collected, and raised to adults which were then fed on a clean beast. No clean ticks were available at that time. The cattle used in the transmission experiments were either reared under tick-free conditions at the laboratory or obtained from farms free from East Coast fever and where dipping was regularly practised.

The cattle were not always free from other tick-borne parasites. In some cases *Anaplasma* was demonstrated in blood smears, and in a few others, *Theileria mutans* was observed in the blood for several weeks prior to the feeding of the ticks. Nevertheless, the presence of these parasites does not affect the validity of our deductions on the transmission of virulent *T. parva* by the different species of ticks.

TRANSMISSION EXPERIMENTS

Rhipicephalus appendiculatus

We experienced no difficulty in transmitting East Coast fever with nymphal and adult ticks that had fed as larvae and nymphae respectively on an infected animal. Larvae, hatched from eggs of females engorged on infective blood, did not transmit the disease when fed on a clean beast. Nymphae infected as larvae invariably produced East Coast fever in clean animals; adults developed from these nymphae proved free from infection, thus confirming that infective nymphae clean themselves of *Theileria parva* in the process of feeding.

Experiments on interrupted feeding at different intervals are in progress; and we hope to ascertain whether infective nymphae which have only partially engorged at the time of death of an East Coast fever animal will, at different

short intervals, again convey the disease to another animal. Lounsbury's observations on transferred ticks are not without interest, although he (1903) expresses the belief that the infectivity of the transferred ticks depended on the feeding of their larval or nymphal stage. Nuttall & Hindle (1913) have dealt with the effect of incomplete feeding on the infectivity of *Rhipicephalus appendiculatus*. They state: "Our attention was first directed to this subject by Colonel H. Watkins-Pitchford, F.R.C.V.S., who informed us that, in Natal, he had been able to infect cattle with East Coast fever by the bites of ticks that had previously fed for two or three days on a normal animal. His experiments, which have never been published, showed that ticks do not necessarily become 'clean' as a result of biting a vertebrate host, and the importance of this discovery is such that we decided to repeat and also, if possible, extend Watkins-Pitchford's observations in Natal."

These authors add: "Our experiments entirely confirm his discovery and, moreover, demonstrate that an infected tick does not become infective until it has fed for at least two days." Walker (1930) carried the last observation further and found that "an infected adult tick transmits East Coast fever only after it has been biting for a period of not less than sixty hours, and is then only infective for a period of sixty hours, so that after the lapse of 120 hours it can no longer transmit the disease".

The passage of the parasite from nymphae to adults has been confirmed in many of our experiments when males and females together, and when only males, were fed on a "clean" beast. Theiler (1907) showed in one of his experiments that East Coast fever could be produced by feeding infected males ("nine brown male imagines") on a normal ox. We repeated this experiment with male *R. appendiculatus* reared as follows:

Adult ticks engorged on a clean bovine on 23. ix. 35; oviposition began on 28. ix. 35; eggs hatched on 21. x. 35, and the larvae were fed on a hare on 29. x. 35. The larvae dropped, replete with blood, from 2 to 4. xi. 35 and moulted to nymphae from 10 to 12. xi. 35. The nymphae were then placed on bovine No. 763 reacting to East Coast fever and with numerous parasites (Koch's bodies and piroplasms) in the blood. From 1 to 9. xii. 35 the nymphae dropped; and they moulted to adults from 17 to 27. xii. 35. The males were collected and placed on bovine No. 1366 on 2. i. 36. The beast showed first rise in temperature on 14. i. 36. Koch's bodies appeared in gland smears on 17. i. 36 and the beast died of East Coast fever on 23. i. 36. The males were taken off the host and died within 2 days. Theiler (1905) observed that the males of the bont-tick (*Amblyomma hebraeum*) remain many months on the same host. He adds: "this is not a peculiarity of the bont-tick; the males of almost every species may do so. Once they are removed, however, from the host they soon die." In Nuttall & Hindle's experiment (1913) nymphae that had fed for 2 days were removed and kept for further experiment. At a period of 16 and 19 days, all but six had died.

We have not fully investigated the significance of incompletely fed ticks

in relation to the transmission of East Coast fever, and the incidence of the peculiar outbreaks of the disease in Kenya. We have raised these points because they may have some, albeit a remote bearing on short-lived sporadic outbreaks of the disease in the field. The males, in virtue of their habit of feeding more than once on a beast they themselves had infected with *Theileria parva*, will again take up the parasite during its development in the host. The fate of the parasites imbibed at this stage is unknown; but in the majority of cases, apparently, the tick would soon die on leaving the host. Partially fed females—and apparently nymphae which have not fully engorged—do not die so readily as the males. If these ticks were removed from an animal before cleaning themselves, they would survive for some time, and during that period might provide a source of infection.

An experiment by Nuttall & Hindle (1913), however, showed that "the partial feeding of infected ticks for two days, followed by starvation for seventeen days, renders them non-infective". This conclusion was arrived at as a result of a single experiment:

Two batches of infected nymphae were fed on calves for 2 days. One lot of fifteen ticks and another of nineteen ticks were then removed and kept at room temperature (about 20° C.) for 18 and 15 days respectively. Both lots were kept overnight at 37° C. and placed on a calf. Only six nymphae survived; they fed to repletion. The calf did not contract East Coast fever, although later it was proved to have been susceptible. The authors continue: "Although the number of ticks (six) used in this experiment is rather small, Theiler, Gonder and other observers, are all agreed that practically 100 per cent of *R. appendiculatus* become infected when fed on an infected animal. Therefore, it seems that ticks lose their infection within seventeen days of ingesting blood, and we are led to assume that the developmental processes started by the ingestion of blood into the ticks, continue, even if the latter is removed from its host prior to being fully engorged. Apparently, however, when once started, this development of the parasite results in its own destruction, unless it is able to enter the blood of a bovine animal within a period certainly less than seventeen days."

Clearly it was necessary to confirm this, if possible, particularly in view of the fact that later investigations indicate that not every tick fed on an infective animal is capable of transmitting the disease.

We have used various numbers of nymphae and adults of *R. appendiculatus* to transmit East Coast fever with the intention of studying differences (if any) in the incubation period, and in the course and the severity of infection. No significant differences have, so far, been observed in the disease produced by a few (5 to 15) ticks and that transmitted by larger numbers (50 to 100) of ticks. Lounsbury (1906) showed in one experiment that it was possible to infect an animal with one adult *R. appendiculatus*. In several others, transmission was effected with batches ranging from two to fifteen brown ticks. Walker (1931) infected nineteen susceptible beasts each with ten ticks from

proved infective broods; thirteen animals (or 68 per cent) contracted the disease. Infestation with lots varying from twelve to twenty ticks produced East Coast fever in three (or 37·5 per cent) out of eight cattle. Larger numbers (100–175 ticks) placed on two animals gave a 100 per cent infection. Nuttall & Hindle, we have already stated, considered that "practically 100 per cent of the ticks which imbibe the parasites are provedly infective". Cowdry & Ham (1932) were unable to confirm this; they claim that "approximately accurate figures on the survival of ingested parasites can only be secured from sections. Of the 290 ticks of our standard series examined in very complete serial sections, parasites were found in 178, or 60·1 per cent. In the first series of infective nymphae, in which we kept records of sex, 33 per cent of the ticks containing parasites were females, and 66 per cent were males."

In preparing our infective ticks we have been particularly careful to place "clean" batches on a beast only when gland and blood smears demonstrated heavy infestation with *Theileria parva*. We have borne in mind Cowdry & Ham's (1932) observation that not all the parasites imbibed with the blood develop in the tick. In all our observations the parasites have first appeared in the ear glands on the first day of fever. Koch's bodies and piroplasms were found in the body glands and the blood usually later—from about the fourth day onwards. Sometimes, both Koch's bodies and intracorpuscular piroplasms were consistently rare throughout the febrile reaction. This is not infrequently the case in animals which survive infection. Infestation of cattle with a small number of ticks may at times prolong the incubatory period of the disease and can perhaps be explained on the basis of Cowdry & Danks's life cycle of *T. parva* in cattle. A small number of ticks, possibly some of which do not contain parasites, introduce into the vertebrate host only a small number of infective organisms or sporozoites. These few parasites enter the lymphatic system to multiply prior to invading the blood stream; and the point of saturation and general dispersal is prolonged.

The influence of temperature on the tick host and on the parasite within the tick has been studied by Theiler (1909) and by Nuttall & Hindle (1913). The former exposed infected nymphae of *Rhipicephalus appendiculatus* to a temperature of 0° C. for half an hour daily for 21 days. He found that engorged nymphae exposed to this temperature moulted in 46 days after collection, whereas the control nymphae kept in Petri dishes at a normal temperature moulted 32 days after collection. Theiler fed the cooled ticks on a clean animal to which they transmitted East Coast fever. He concluded, therefore, that a temperature of 0° C. does not interfere with the development of the parasite within the engorged nymphae; nor does it kill the virus contained in the engorged nymphae of *R. appendiculatus*. Nuttall & Hindle cite Theiler's experiments, an account of which must have appeared in a publication different from that available to us, for they remarked, "It may be noted that Theiler (1909) exposed ticks infected with East Coast fever to varying degrees of cold for different periods"; they quote his conclusions to which we have

just referred and also that: "In no instance was any difference noted in the virulency of the disease; the only point of interest was that the ticks kept at a low temperature moulted at a later date than the controls, but when the former were placed on susceptible cattle these animals promptly contracted the disease and died." Nuttall & Hindle point out: "Theiler does not give any particulars of his experiments and we are unable to explain the discrepancy between his results and those obtained in our experiments."

It seems to us that the discrepancy between the two results may be explained by the difference in the time for which the ticks were exposed. Nuttall & Hindle kept their infective nymphae at a temperature of 10° C. *continuously* for 3 weeks and placed them without previous warming on a calf in the cold stall at ordinary outdoor temperatures (about 8° C.). Theiler, as we have stated above, exposed his ticks for half an hour daily. The nymphae (in Nuttall & Hindle's experiments) did not transmit East Coast fever. In a second experiment some of the infected nymphae exposed to 10° C. for 3 weeks were again kept at a temperature of 20° C. for a period of 4 weeks, and finally for 2 days at 30° C. They were then placed on a calf that contracted East Coast fever 13 days later and died of the disease on the fifteenth day. Summarizing these particular experiments, the authors state: "(6) Infective ticks are rendered non-infective by exposure to a temperature of about 10° C. for three weeks. (7) Their infectivity may be restored by subsequently warming them."

The investigations of Nuttall & Hindle were still in progress when these interesting records were published. We can find no further communication on these lines. They are of sufficient interest to warrant extensive and more exhaustive study, and the results may help to a better understanding of the disease and its inexplicable occurrence in certain areas at high altitudes.

Nuttall & Hindle showed that, in their experiments, the development of the parasite was arrested when infected nymphae were exposed to low temperature for a continuous period of 3 weeks. The nymphae engorged and ultimately moulted to adults without cleaning themselves of infection in the accepted manner. Will the resultant adults, therefore, transmit the disease in some form or other; or will the parasite in the nymphae be destroyed by the ingestion of blood? Will the effect of low or very high temperature vary in any particular stage in the development of the parasite? Cowdry's explanation of the development in the tick might form a basis for such an investigation. Possibly, exposure of infected ticks to alternate degrees of temperature (simulating diurnal variations) may affect the parasite differently from exposure to a continuous and more directly cumulative temperature.

It is a widespread belief that East Coast fever cannot exist for a prolonged period in the cold atmosphere at high altitudes, and that the common vecting tick (*R. appendiculatus*) cannot survive and become established in these areas.

Field observations in South Africa and in some parts of Kenya seem to bear out this belief. At times, however, small outbreaks that cannot easily be explained by movement of stock alone do occur at altitudes of over 7000 ft.

in this colony. Some of these are short lived and the mortality is often low. Others have been known to persist for many months, and the tick vector can nearly always be found.

We repeated the experiments of exposing infected batches of *R. appendiculatus* to different temperatures and humidity with a view to throwing some light on these peculiar sporadic outbreaks in high country.

Numerous larvae were fed on a reacting bovine. After moulting into nymphae, the ticks were divided into three main groups. Each group was again divided into several lots. The first main group of infective nymphae were exposed to the following conditions for 1 week: (*a*) to a temperature of 4–6° C.; (*b*) to a temperature of 8–10° C.; (*c*) to a temperature of 35–38° C.; (*d*) to a temperature of 4–6° C. for 12 hours followed by exposure to 19–20° C. (room temperature) for 12 hours for the whole week; (*e*) to a temperature of 8–10° C. alternating with a temperature of 19–20° C. for each day of the week; (*f*) to a daily, alternating temperature of 8–10° C. and 35–38° C.

The second main group of infected nymphae was exposed to the same conditions ((*a*) to (*f*)) but for a total period of 15 days. The third main group contained four lots of infected nymphae that were exposed for 3 weeks to: (*a*) a temperature of 4–8° C.; (*b*) a temperature of 8–10° C.; (*c*) an alternating temperature of 4–8° C. for 12 hours followed by 18–20° C. for the other 12 hours of each day; and (*d*) a temperature of 8–10° C. for 12 hours followed by 18–22° C. for 12 hours daily.

The number of nymphae in each lot was never less than 110 and never more than 200. Not all the ticks survived exposure. The hot temperature was definitely less favourable than the cold or the moderate temperatures. In one case, only seven out of 120 ticks survived 14 days at a consistent temperature of 35–38° C. Another lot of 134 nymphae in the alternated (12-hour) temperature of 8–10° C. and 35–38° C. all died within a fortnight.

The ticks were placed on known susceptible bovines at the end of the appropriate periods. The cattle were kept in clean stalls with an average maximum (or day) temperature of 21° C. and an average minimum (or night) temperature of 10° C. All ticks were placed on the ears of the cattle immediately they were taken out of the incubating, or cold room, chambers. A strong ear bag was tied round the ears and the ticks prevented from escaping. The temperature within the ear bags was approximately 36° C.

The ticks did not always attach themselves and start feeding within a short period. All, however, began to feed within 24 hours with the exception of one batch exposed to alternating temperatures of 8–10° C. and 35–38° C. for 15 days. None of these ticks (nymphae) fed on the bovine. One lot of ticks exposed to a temperature of 35–38° C. for 15 days did not feed well; only seven replete ticks dropped off, and the beast on which they fed did not react to East Coast fever.

All other animals used in this experiment contracted East Coast fever and died of the disease. We are thus able to state that exposure of unfed, infective

nymphae to cold temperatures for periods of 1, 2, or 3 weeks does not always destroy, nor affect the development of, *Theileria parva* in the tick host as shown by the ability of the tick to transmit the normal disease.

We cannot, therefore, confirm the experience of Nuttall & Hindle (1913), but endorse the statements made by Theiler (1909). We extend the observations. Our experiments indicate that warm temperatures and alternating temperatures for the periods already mentioned do not affect the parasite in the tick; they, more than cold temperatures, seem to be inimical to the tick itself. We are continuing these experiments in order to estimate the relation of humidity and other climatic factors on the invertebrate host and the parasite. Theiler (1921) states that "Experience has proved that the cold in itself is not a barrier to the development of the blue and red ticks in the high veld" of South Africa. We feel justified in making a similar remark with regard to the brown tick, *Rhipicephalus appendiculatus*.

That recoveries occur from East Coast fever transmitted by ticks is well known; and for the purposes of this preliminary account we include records of such a case:

Nymphae, of *R. appendiculatus*, infected as larvae were placed on a clean bovine No. 8943 on 21 October 1935. The ticks fed to repletion and dropped from 26 to 29 October. The animal contracted East Coast fever, showing the first rise of temperature on 12 November. Koch's bodies and piroplasms were rare on the 14th and had disappeared on the 17th; on the 18th a few small piroplasms were again observed in blood smears, but after that date no parasites were seen, and the beast recovered. Exposure to further infection, 6 weeks later, proved that the animal was immune.

In the *Annual Report of the Chief Veterinary Research Officer for the year* 1934, reference is made to the transmission of East Coast fever by ticks (*R. appendiculatus*) taken from a beast suffering from turning sickness. One of us (Lewis), in collaboration with Mr J. R. Hudson, collected a large number of engorged nymphae from this animal. Replete ticks dropped from 10 to 12 September 1934; they moulted to adults between 18 and 29 September. Adults were placed on a clean bovine No. 8772 on 28 September; and fifty-one fully fed females dropped from 8 to 14 October. The animal showed a first rise in temperature (103° F.) on 24 October, or 26 days after the ticks had been placed on the beast. Koch's bodies and piroplasms appeared in gland and blood smears respectively on 25 October, and the animal died of East Coast fever on 28 October.

In view of Mettam & Carmichael's (1936) statement that ticks, presumably taken from a turning-sickness animal, failed to transmit turning sickness when fed on a recovered East Coast fever beast and that such ticks failed to infect clean calves with East Coast fever, we feel with Daubney (1936) that the transmission experiment to which we have referred needs confirmation.

Rhipicephalus capensis

Lounsbury (1906) writes of this species as being the most common of the brown ticks in the Cape Colony. It occurs in all coastal districts as far west as Cape Town; the adults often swarm in the tail-brush, on the dewlap, and on the under parts. Nymphae, like adults, feed readily on cattle; and he remarks: "Should East Coast fever ever reach the south-western districts of the Colony, the Cape and the shiny brown tick would, doubtless, be agents to spread the disease." That this species of tick is capable of transmitting East Coast fever was proved by Lounsbury's experiments late in 1904 and again in 1905; and Theiler (1907) verified the results.

We collected large numbers of engorged, female *R. capensis* from cattle near Lake Naivasha and at Lumbwa, Kenya Colony. We failed to feed sufficient larvae to enable us to carry out experiments. Further attempts are being made, however, in order to ascertain whether the *capensis* frequently found in our "clean" areas, but which differs in some respects from the South African species, is an important agent in the transmission of East Coast fever.

Rhipicephalus evertsi

This species was incriminated in the transmission of East Coast fever by Lounsbury (1906), Theiler (1907) and by Stockman. The last-mentioned investigator carried out his experiments in England, and we are indebted to Theiler's publication for the information. Montgomery (1913) did not succeed in producing the disease with this tick "although", he adds, "in South Africa *R. evertsi* has been found culpable on a very few occasions".

We are again able to confirm that *R. evertsi* can act as an agent in the transmission of the disease.

Several engorged females of this species were collected on 15 February 1935, from a sheep on the Experimental Station at Naivasha.

Oviposition began on 1 March, and the eggs hatched on 29 March. Larvae were placed on an East Coast fever reacting beast, No. 448, on 8 May; they were engorging on the 12th and began to moult on the 17th; many nymphae dropped engorged a few hours before the animal died on 20 May. Other, partially fed nymphae crawled off after death, and when tested for infectivity, failed to transmit East Coast fever. Only thirteen adults emerged from the moult of engorged nymphae. These adults were placed on a clean bovine No. 589 on 9 July; they dropped from the 18th to 21st. Five males were taken off, and died soon after. Bovine No. 589 showed a rise in temperature on 21 July and died on 2 August, when numerous Koch's bodies and piroplasms were found in smears from gland, blood and spleen. Post-mortem examination confirmed the diagnosis.

Rhipicephalus pulchellus

Although we have been able to feed larvae, nymphae and adults of this species on cattle, sheep and on hares, we, like Montgomery (1913–15), have

not succeeded in transmitting East Coast fever with the immature ticks; and several efforts with adults have also failed.

Rhipicephalus sanguineus

In 1909 Dschunkowsky & Luhs seemed to incriminate *R. sanguineus* as a vector of *Theileria annulata*, the causal organism of "tropical piroplasmosis" of cattle in Transcaucasia. The tick is not often found on cattle in Kenya Colony; in fact, only on a few occasions have very small numbers been collected from this host. Nevertheless, we endeavoured to feed numerous nymphae on a bovine reacting to East Coast fever. Out of 200 nymphae, only five fed; and these did not transmit the disease when, as adults, they were placed on a clean beast. Further attempts are now being made.

Rhipicephalus simus

In 1904, Theiler (1905) collected larvae of *R. simus* from an ox 2 days previous to its death from East Coast fever. Nymphae reared from these larvae transmitted the disease to a clean beast that died from the infection. Lounsbury (1906) transmitted "infection from two cases by *R. simus* adults to three animals" in May and June 1905.

In our one experiment with this tick we produced the disease in an animal that recovered from the infection. Many engorged adults were collected from a dog on 6 August 1935; oviposition commenced on the 23rd; larvae emerged from the eggs from 6 to 15 September. The larvae were fed on a field rat, *Arvicanthis abyssinicus*, on 17 September; they dropped engorged from the 21st to 22nd; and moulted to nymphae on the 29th and 30th. On 2 October, 100 nymphae were placed on bovine No. 762 at the height of reaction to East Coast fever; they dropped from the 6th to 12th and moulted to adults on 28 October. The adults were then fed on a normal bovine No. 765 on 14 November, and they were collected, fully fed, from 29 November to 3 December 1935. Bovine No. 765 showed first rise in temperature on 28 November (14 days after the ticks were placed on the beast); and Koch's bodies were found in gland smears on 1 December. Koch's bodies were more numerous on the 2nd and 3rd, and appeared in the blood stream from the 4th to 7th, after which no parasite could be demonstrated. The beast recovered normal temperature on 15 December. Bovine No. 765 was then exposed to artificial and natural infection and proved immune to East Coast fever.

Amblyomma hebraeum and *A. variegatum*

South African experience with *A. hebraeum* indicates that it is not an agent in the transmission of *Theileria parva*. The tick does not occur in Kenya, but seems to be replaced by *Amblyomma variegatum*, a species with a wide distribution in the colony. Up to the present we have attempted transmission only with adults which have been fed as nymphae on a diseased animal. Our results, so far, are negative.

Boophilus decoloratus

Lounsbury and Theiler were unable to incriminate this tick as a vector of East Coast fever, and we have not yet carried out experiments with it.

Hyalomma spp.

Tick species of the genus *Hyalomma* are sometimes difficult to identify with accuracy. The morphological differences are often so small and variable that without detailed and, not infrequently, prolonged examination, it is impossible to ascertain whether specimens belong to one variety (or subspecies) or another. The genus has been revised by Schulze & Schlottke (1930) and, more recently, by Schulze (1930). Delpy (1936)[1] has also dealt with the classification of this genus in so far as *H. dromedarii* is concerned. In the first publication the authors point out that, apart from the tortoise tick "*syriacum* Koch", the majority of *Hyalomma* spp. that have been found on cattle, horses and mules and similar animals, have been designated *H. aegyptium* Linn., although no one really understood what Linnaeus's species represented. The authors maintain that Linnaeus's amplified description of 1764 shows clearly and distinctly that by it only the present type *H. syriacum* Koch can be understood, and that the description is admirably suited to its male, but to no other type.

The tick that has so widely been named *H. aegyptium* may, therefore, be referred (according to Schulze & Schlottke) to a number of varieties; but as the classification is based on characters sometimes difficult and very troublesome to ascertain, it seems desirable to obtain further evidence from the characteristics of the immature forms supported by possible biological differences.

We have examined the specimens with which we experimented and have also consulted Prof. Schulze to whom we are grateful for the determination of the species according to the revised classification. We have not been able to ascertain the exact identity of the species or variety of *Hyalomma* that has been associated with animal diseases in the past. It suffices the purpose of this paper that *Hyalomma* ticks are referred to.

Apart from their importance as parasites of domestic animals, the important part played by *Hyalomma* spp. in the transmission of animals' diseases has not been fully investigated.

Brumpt (1920) states that Carpano (1915)[2] considers *H. aegyptium* to be the tick vector of the parasites (*Theileria parva* and *T. mutans*) of the "Mediterranean Coast fever". This tick normally lives in the larval and nymphal state on rabbits, hares, birds and the hedgehog, on which they were unable to take up

[1] Delpy, L. (1936). Notes sur les Ixodidés du Genre *Hyalomma* (Koch). *Ann. parasit. hum. comp.* **14**, 3, pp. 206–215.

[2] Carpano, M. (1915). La febbre della costa Mediterranea. Piroplasmosi tipo 'parvum' nei bovini del basso bacino del Mediterraneo. *Ann. d' Ig. Sperimentale*, **25**, N. Ser. No .4, pp. 342–410.

these piroplasms. In nature, the tick is encountered on cattle in the adult stage. Experimentally, Brumpt was able to rear larvae of certain broods, and to raise them to nymphae.

Warburton (1923), dealing with *Hyalomma aegyptium* and its relation to disease in a contribution to the *Encyclopaedia of Veterinary Medicine, Surgery and Obstetrics*, states: "There is at present no definite proof that *H. aegyptium* is pathogenic, but there is a strong suspicion that it transmits *Nuttallia equi*, the cause of biliary fever in horses, there being a remarkable agreement between the distribution of the species and the incidence of the disease in Africa, Asia and South Europe. In any case the tick is so abundant as to be distinctly injurious to domestic animals."

Bellitzer (1925) reports that *Nuttallia equi* is transmitted by *Hyalomma aegyptium* in European Russia; Cooper (1926) remarks that "experience indicates that all cattle in India are infected with *Theileria mutans* transmitted by *Hyalomma aegyptium*"; and Kalashnikov records that "in Astrakhan piroplasmosis is said to be transmitted by this tick". Sergent and his colleagues (1928*a*) have shown that adults of *H. mauritanicum* (or *H. detritum mauritanicum*) transmit north African theileriasis, a disease caused by *Theileria dispar*. du Toit (1931), referring to this discovery, states: "It should be mentioned that this is the first time that a species of *Hyalomma* has been found capable of transmitting a disease." In the same year (1928*b*), Sergent and his fellow-workers showed that *H. lusitanicum* Koch (or *anatolicum* Koch) transmits anaplasmosis of cattle. Rosen (1931), in his observations on theileriasis (*Theileria annulata*) during an epidemic of the disease, believed the outbreaks to have been due to the ticks *Hyalomma aegyptium* and *Boophilus* sp. that were introduced to the Jordan Valley on imported barley straw. We might mention that Carpano (1932) concluded from his observations on *Trypanosoma theileri* in cattle that *Hyalomma aegyptium* was the vector of the disease; and that Borzenkov & Donskov (1933) succeeded in transmitting plague to ground squirrels through the medium of *H. volgense*. Returning to cattle diseases caused by *Theileria* and transmitted by *Hyalomma* spp., we have the observations of Galuzo (1934) who, from experiments and field observations in 1928–9, showed that in central Asia *Theileria annulata*[1] is transmitted by *Hyalomma dromedarii asiaticum*[2] P. Sch. & E. Schl., and though this species was not found in Armenia in 1931, all the ticks collected in the locality where an epizootic of the disease occurred belong to the genus *Hyalomma*.

Meyer (1931), in his discussion on the relationship of *Theileria annulata* and *T. dispar*, expresses his opinion that "the latency of the parasites in the pre-immunized animals and its significance in reinfection deserve further investigation. Not the inoculation diseases but the infections induced by the tick *Hyalomma mauritanicum* or other transmitters must be compared"; and

[1] Galuzo (1935) concludes that *Theileria annulata* is transmitted by *Hyalomma detritum rubrum* in Kazakstan and Tadjikistan, Russia.

[2] Delpy (1936) considers this variety to be a synonym of *Hyalomma dromedarii*.

du Toit (1931), differentiating the different *Theilerias* of cattle includes, as a chief difference between *T. parva* and *T. dispar*, that the former parasite is carried by *Rhipicephalus* spp. and not by *Hyalomma*.

Hyalomma aegyptium

The tick considered under this name and also as *H. aegyptium aegyptium* (Linn.) by Bedford (1932) is, according to Theiler (1905), a very common South African parasite, and is found under the same conditions as the red tick, and often in company with it. Lounsbury investigated its life history, and while the larvae would not feed on any mammal, they fed on fowls, on which they underwent the first moult. The nymphae drop in about 10 days, and the adults readily feed on cattle.

Theiler (1905) infested an animal with numerous adults of *H. aegyptium* removed from an ox 2 days previous to its death from East Coast fever. The experimental animal did not contract the disease. What further trials were made with this tick it is not possible for us to state. In a farmers' bulletin (No. 7 of 1911) Theiler explained that "the bont-legged tick (*H. aegyptium*) has not been discussed here as it has not yet been proved to act as a carrier of the disease"; and in a revised article, published in the *Journal of the Department of Agriculture, Union of South Africa* (1921) and also issued as Reprint No. 6 of 1921, Theiler writes of *H. aegyptium*: "Although not a disease-transmitting tick, it frequently is the cause of lameness in sheep and goats, the adult attaching itself between the hoofs, it is sometimes known to produce ulcerating sores in cattle."

Hyalomma impressum near *planum* P. Sch.

Bedford (1932) states that this species of *Hyalomma* is very common and widely distributed in South Africa. Apparently no attempts have been made to transmit East Coast fever with it. Lewis (1932), dealing with the life history of *H. aegyptium impressum* erroneously under the headings, *H. aegyptium* (Linn. 1758) Koch, 1844 and *H. impressum albiparmatum* Schulze & Schlottke, 1930, found this variety also to be a two-host tick on the hare and a three-host tick on cattle and sheep. It is a common parasite of cattle in the colony, adults being the usual specimens collected from domesticated animals. Larvae and nymphae are sometimes found on cattle, sheep and goats.

Before proceeding with transmission experiments the adult ticks were examined and identified, and we satisfied ourselves that we were dealing with but one variety of tick, namely: *H. impressum* near *planum* P. Sch. We observed also that the larvae did not always feed readily on cattle; sometimes a high percentage of those placed on the ears of a bovine would feed to repletion; at other times only a dozen or so, out of many hundreds, would

engorge. The others crawled about the ear and in the ear bag, and died in a few days.

After many attempts to feed the larvae on an East Coast fever animal, we succeeded in obtaining large batches of replete larvae. Nymphae fed very well in most cases, and the adults always.

On many occasions we have succeeded in transmitting East Coast fever with nymphae and adults of *H. impressum* near *planum* P. Sch. that had previously fed as larvae and nymphae respectively on a diseased bovine. Here, however, we shall give details of one complete series of experiments only.

TRANSMISSION BY NYMPHAE WHICH HAD FED AS LARVAE ON AN INFECTED ANIMAL

Larvae taken from a series of ticks that had been reared through several generations, and at each stage fed on a hare, were placed on an East Coast fever reacting bovine, No. 1363, on 1 February. Numerous engorged larvae dropped from 3 to 13 February 1936, and they moulted to nymphae from 12 to 20 February. Nymphae were allowed to harden and a batch of thirty was placed on a known clean beast, No. 1452, on 24 February. Twenty nymphae fed to repletion and dropped from 2 to 5 March 1936. On 17 March, numerous Koch's bodies were observed in gland smears; they were also numerous on the 18th and 19th; on the 20th they were less frequent, and thereafter disappeared. Agamogenous and gamogenous Koch's bodies were observed in the glands; but neither piroplasms nor Koch's bodies appeared in the blood smears throughout the short reaction period. The beast recovered on 25 March; its immunity to the disease was tested artificially and by natural exposure, and the animal still survives. It may be noted that no glands other than those at the base of the ear on which the ticks were placed showed any swelling or Koch's bodies at any time. Even this swelling lasted only for a few days and then subsided.

The nymphae were collected, allowed to moult to adults which were tested for cleanliness and found free from infection.

Another lot of larvae, bred from adults that had been fed on a hare, were placed on bovine No. 448, at the height of a reaction to East Coast fever, on 8 May 1935; they dropped from 10 to 20 May, and moulted to nymphae from the 24th to 29th. A hundred were placed on clean bovine No. 582 on 14 June 1935. Fifty-two ticks fed to repletion and dropped from 18 to 24 June.

The animal showed a rise in temperature on 28 June: Koch's bodies were rare in gland smears on the 30th and piroplasms and Koch's bodies were numerous in the blood from 6 July to the time of death on the evening of 13 July. Post-mortem examination confirmed the microscopic findings and clinical diagnosis of East Coast fever.

Adults moulted from the engorged nymphae again proved free from infection.

Transmission by adults that had fed as nymphae on a diseased animal

Adults of *Hyalomma impressum* near *planum* P. Sch. were fed on a clean calf, and dropped engorged from 20 to 26 September 1935. Oviposition began on the 26th and hatching took place from 23 to 25 October. The larvae were placed on another susceptible bovine, No. 78, on 30 October and large numbers of replete ticks were collected from 2 to 8 November. All had moulted by the 13th. The resultant nymphae were put on the ears of bovine No. 763 on 1 December 1935, when Koch's bodies (agamonts and gamonts) and piroplasms were abundant in the circulatory system.

Eighty-three (out of 100) nymphae fed and dropped on 8 and 9 December. They moulted to adults on the 27th. The adults were placed on susceptible bovine No. 1363 on 8 January 1936, and all had dropped by the 21st.

The animal showed the first rise in temperature on 21 January, and after a prolonged reaction period of 23 days died of East Coast fever on 12 February 1936. The time taken from the date the infected adults were placed on the beast to the day on which the animal died was 35 days, the incubation period being 13 days.

An experiment to test the passage of *Theileria parva* through the eggs of *Hyalomma impressum* near *planum*

Adults from a known clean batch of ticks were fed on East Coast fever reacting bovine No. 765 on 3 December 1935, when Koch's bodies and piroplasms were numerous in the blood. The ticks dropped fully fed from the 9th to 16th and were ovipositing from the 16th to 18th. Hatching took place from 13 to 22 January 1936. The larvae were placed on bovine No. 1395—proved to be free from infection—on 1 February 1935. Numerous larvae fed and dropped from 6 to 11 February. Bovine No. 1395 showed no febrile reaction, and when later exposed to infected ticks, proved susceptible to, and died of East Coast fever.

Summary

1. Investigations into some of the problems associated with African East Coast fever and its vectors have been undertaken: and although these are, as yet, incomplete we consider them of sufficient interest to warrant their publication at this stage.

2. The present position regarding the distribution of certain tick species in relation to East Coast fever in Kenya is briefly reviewed; and outbreaks of what may be peculiar forms of the disease in sporadic areas are mentioned.

3. It is thought that the passage of *Theileria parva* through different

species of ticks might throw light on some sporadic outbreaks of the disease and on the peculiar character of some of the cases encountered.

4. Transmission by nymphae and adults of *Rhipicephalus appendiculatus*, by adults of *R. evertsi* and *R. simus* is confirmed. Experiments with *R. sanguineus*, *R. pulchellus* and *Amblyomma variegatum* were negative.

5. Exposure of infective nymphae of *Rhipicephalus appendiculatus* to different degrees and conditions of temperature prove that the ticks remain infective after being subjected to 4–6° C., and 8–10° C. for 1, 2 and 3 weeks. Exposure to different alternating temperatures for similar periods had no effect on the virulence of the parasite. The ticks exposed to warm temperatures (35–38° C.) did not survive to the same extent as those exposed to cold temperatures. Ticks that survived for 1 week transmitted the disease.

6. Animals that ultimately recover from artificial infection may show a mild thermal reaction during the short course of the disease without showing typical clinical symptoms. In such cases diagnosis is frequently difficult, and Koch's bodies may be rare.

7. The association of *Hyalomma* spp. with many different diseases is briefly dealt with; and it is shown that *Hyalomma impressum* near *planum* P. Sch. is capable of transmitting East Coast fever in the nymphal and the adult stages after the larvae and nymphae respectively have fed on an infected animal. The parasite does not pass through the egg. *H. impressum* near *planum* is common in most parts of Kenya Colony.

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PARASITIC LARVAE IN *BOMBUS TERRESTRIS*

By M. M. LEGGE, A.R.C.S., B.Sc.

(With 5 Figures in the Text)

I wish to record some unidentified parasites, from the abdominal cavity of a Queen Bumble-bee (*Bombus terrestris*).

Thirty-three sausage-shaped parasites, each about 3–4 mm. long, were found lying loose in the abdominal cavity, amongst the gut and the much-reduced ovaries. One of them was filling a circular hole in the left ovary. In spite of this heavy infestation the bee was alive when caught.

The general structure, which shows them to be hymenopterous larvae, is as follows:

(1) Apparently no spiracles.

(2) Mandibles small and far apart.

(3) No facial struts supporting mouthparts. No labial or maxillary palpi. No antennae.

(4) Complete tentorium.

(5) Soft transparent cuticle.

(6) A pair of large labial (silk) glands. These open near the mandibles, and extend backwards and laterally for a short distance, until they bifurcate, the four branches ending at the posterior end of the stomach. Just beyond their terminations are a pair of small spherical structures.

(7) The gut: the narrow muscular pharynx leads through a valve-like constriction into a large stomach, which is joined on to the hindgut by an apparently solid cord of cells. Probably these larvae are in their last instar, and the connexion between the stomach and hindgut is about to be formed.

The hindgut gives off two long lateral diverticulae, which project forwards.

These parasites have been examined by Mr G. C. Varley, who is making a comparative study of hymenopterous larvae, and he considers that the large labial glands and the size and position of the mandibles indicates that they are neither Chalcids nor Proctotropids. The presence of these glands suggests that they are Ichneumonids or Braconids, but the absence of facial struts refutes this suggestion.

The following hymenoptera, known to be gregarious endoparasitoids, do not resemble my specimens: various pteromalids, *Tetrastichus*, *Lipomastix*, *Apanteles* and *Microgaster*, *Macrocentrus* and *Aphocrita*.

Thus it appears that until the adult stage of these larvae is known, the systematic position of the parasite cannot be determined.

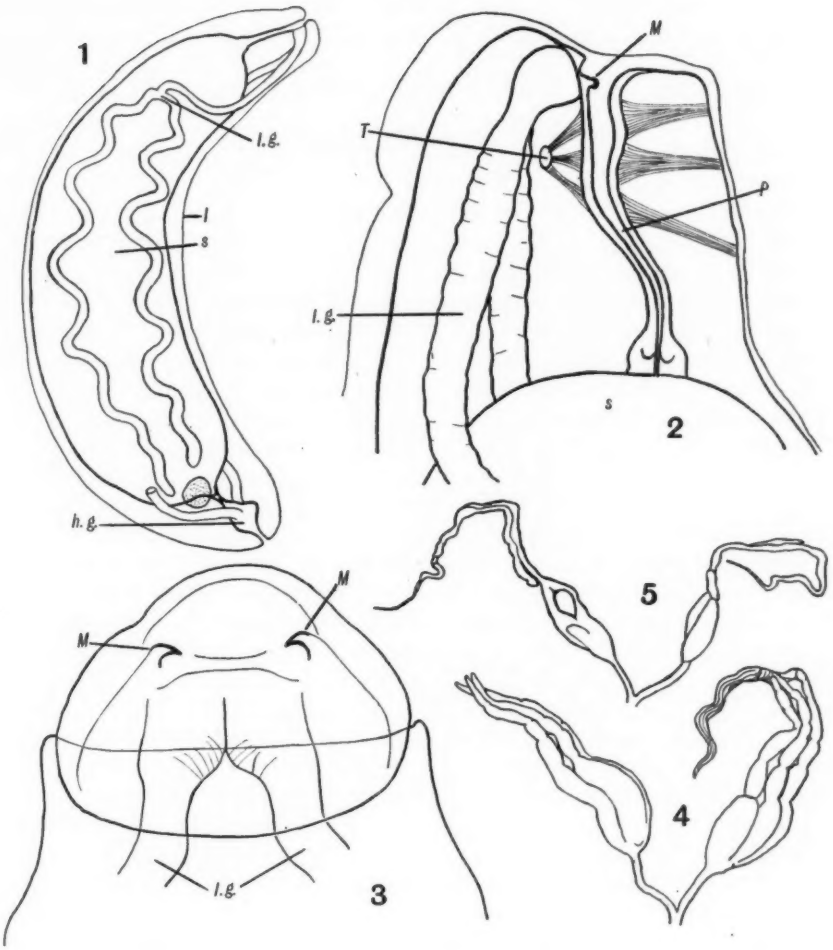

Fig. 1. Lateral view of a parasitic larva from *Bombus terrestris*. *I*. integument; *h.g.* hindgut; *l.g.* labial glands; *s*. stomach.

Fig. 2. Lateral view of head of parasitic larva, showing pharynx, labial glands and mandibles. *l.g.* labial glands; *M*. mandible; *P*. pharynx; *s*. stomach; *T*. part of tentorium.

Fig. 3. Ventral view of head. *l.g.* labial glands; *M*. mandibles.

Fig. 4. Ovaries of a healthy *Bombus terrestris*.

Fig. 5. Ovaries of a parasitized *Bombus terrestris*.

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THE EXPERIMENTAL PRODUCTION OF CUTANEOUS MYIASIS OF SHEEP

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Introduction

The problem of maggot-fly attack of sheep has been, during recent years, the subject of progressive investigation in practically all the sheep-raising countries of the world, and the search for adequate means of control has received much attention, alike at the hands of private investigators, commercial concerns and public authorities. This aspect of the problem has, however, presented the great difficulty in the way of effective research that no reliable method of producing the condition experimentally was known, and investigators were consequently hampered by the capriciousness of natural incidence, the necessity for using very large numbers of animals in each test, and the difficulty of assigning a given effect with any confidence to a single cause in the absence of rigid control of the numerous variables incident on large-scale field experimentation. When smaller numbers of animals have been used so as to be under strictly comparable conditions, it has frequently happened that, at the end of a season's experimental work, the conclusions were found to be invalidated by the failure of the controls to develop a sufficiently high incidence of strike, or by reason of the fact that the experimental groups had such low incidences as to render insignificant any differences between them.

A very important advance was made when Hobson (1935, 1936) showed that oviposition by *Lucilia sericata* on sheep could be induced by treatment of the sheep with chemical attractants. By raising the level of susceptibility to oviposition in all animals under test to a point at which normal individual differences in susceptibility are rendered inoperative, it is possible to obtain reliable comparative data on the repellent effect of dressings, even with small numbers of sheep. The discovery of this method of "attractivation" of sheep is probably the most important practical contribution to the solution of the sheep maggot-fly problem since its terms were first defined by the early investigators.

It is now known, however, that oviposition or "blow" on sheep will not necessarily result in the development of active larval myiasis or "strike". Maldwyn Davies & Hobson (1935) have given evidence to show that the moisture conditions in the fleece are normally unsuited to the survival of eggs or young larvae, and the well-recognized difficulty of producing strike experimentally supports this conclusion. Since many protective dressings rely on a larvicidal, rather than a repellent, effect, the necessity for some reliable means of producing strike becomes apparent.

EXPERIMENTAL PRODUCTION OF STRIKE

Colonies of *L. sericata* were raised in an insectary maintained at temperatures ranging from 10 to 21° C.

Numerous methods of producing strike were tried; the fleece was wetted after oviposition had occurred; pads of moist cotton wool, covered on the outside with cellophane, were sewn over egg clusters on the wool; eggs, first instar, and second instar larvae were placed on the skin and the area wetted. Strike could be obtained by any of these methods, but only in an uncertain percentage of attempts, and they were abandoned.

The method recently described by Freney and his co-workers (Freney *et al.* 1935), makes use of first instar larvae, and is, briefly, as follows:

The skin and fleece of the animal are wetted, and about 2000 first instar larvae are washed on to the area of skin selected for strike. The wool is wetted over this area, and sometimes there is, in addition, a pad of cotton wool placed over it. This method was tried with both first and second instar larvae and with varying degrees of thoroughness in the wetting of the fleece, but failed to give reliable results. It has a further serious disadvantage from the point of view of investigations relating to control. The thorough wetting of the fleece necessary in the method tends to wash out or weaken any substances applied, and thus the testing of a dip or dressing would in itself unfairly handicap the efficacy of the substance under experiment.

The nature of the failures encountered, and a study of numerous natural cases, made it clear that it is not sufficient, for the establishment of myiasis, to have the microclimate of the fleece saturated. In fact this appears to be undesirable. Eggs and young larvae are dependent for survival on a high humidity in the fleece, but as the strike develops, sufficient moisture is provided by exudation from the skin lesion. A lesion does not develop in less than five hours (Davies & Hobson, 1935). Thus the critical period in the development of strike is the initial stage of larval activity. If the fleece is saturated the newly hatched larvae tend to scatter in all directions, all regions being equally favourable in so far as humidity is concerned. They do not remain concentrated in one area long enough to produce a skin reaction. As the fleece gradually dries, all areas become progressively less favourable; under these conditions the larvae are forced to continue their restless migrations, and, unless they chance to find an area of high humidity, from the presence of extraneous organic matter or some such cause, strike does not develop.

It follows, therefore that in the method of general wetting, the body of the fleece must be kept wet for long periods to allow of strike developing, and further, there is no precise control of the site of ultimate establishment of the larvae.

Similarly, it follows that to produce strike at a given point, a limited focus of high moisture content next to the skin, and surrounded by a zone of drier conditions, is desirable. The larvae will thus tend to keep within a circum-

scribed area, and the irritation of their presence will rapidly produce an erythema of the skin. This source of moisture, as the lesion develops, will gradually replace in function the experimentally applied source, which may ultimately be removed. The experimental production of erythema before the eggs or larvae are applied should further ensure success, and should also accelerate the development of strike through increasing the local skin-temperature, and also by facilitating the commencement of tissue lysis.

These objects are achieved in the following manner:

A mild erythema is produced by placing a little water at the base of the wool at the required point, and rubbing the wet skin with the finger over a patch of about half an inch in extent. Larvae are then placed on this patch and a compact plug of cotton wool, which has been soaked in water and the excess lightly squeezed out, is applied over them and held in position by sewing the wool together over it. The plug is generally removed on the second day. This method has proved highly successful, the larvae keeping at first compactly together in an area no greater in size than a shilling piece.

The method of manipulation of the larvae generally used is as follows:

An egg cluster from the insectary is placed in a small petri dish and this is set in a larger vessel containing water and maintained at a temperature of 30° C. The newly hatched larvae crawl out of the Petri dish and drop into the water. They are unaffected by prolonged immersion, and the culture can thus be ignored until it is convenient to use it. The larvae remaining in the dish are washed into the water, which is then strained through fine muslin. The larvae are washed off the muslin into a container. By this method the water volume is reduced and a thick suspension of larvae is obtained, which can be divided into as many portions as are required. The larvae are conveniently transported to the field in water suspension in small vials. The wool is parted and the vial emptied on to the skin at the selected site. The water filters away through the wool and leaves the larvae deposited on the prepared area of skin.

The method of producing strike has also been successfully used with eggs, and, in a few experiments, with second instar larvae reared on meat. These larvae should not be left for more than an hour in water, as they are markedly less resistant to prolonged immersion than first instar larvae.

In the course of experimental testing of various chemicals, over one hundred cases of strike have been produced by this "plug method". Of these, thirty-four were produced on normal, i.e. untreated sheep, and serve as checks of the reliability of the method. The sheep used were Hampshires, Hampshire crosses and Suffolk crosses. The following table shows the number of such control tests and the number of failures:

Stage of larvae	No. of experiments	No. of successes	Remarks
Eggs	15	13	
First instar larvae	19	17 + 2 abortive strikes	In the two abortives, the plugs were removed prematurely
Second instar larvae	6	4 + 1 abortive	

It will be seen from the table that, with eggs, the certainty of success is not quite so great as with first instar larvae. A possible explanation of this lies in the fact that *L. sericata* will lay eggs, even if unfertilized (Evans, 1936). Alternatively, the eggs may occasionally be infertile because of the absence of sunlight, even though artificial light be supplied (Salt, 1932). Neither of these explanations is, however, very probable, since, in the case of experiments with larvae, no batches of infertile eggs were encountered. It is more probable that the eggs shrivelled owing to the plugs drying out before the larvae had hatched, or before the skin reaction had reached the stage of exudative ulceration necessary for their survival.

DISCUSSION

There are now available methods of testing both the repellent and larvicidal properties of dips and dressings against maggot-fly. The method of experimental production of strike described above is highly reliable, easy to carry out on a large scale and allows of great precision in the election of a site, so that, for instance, a small healed lesion of less than an inch in diameter could quite well be tested at will for its reaction to restrike. The method has the great advantage that, unlike the attractivation method for producing blow, it is independent of weather and season. Strikes have been regularly produced at the Cooper Field Research Station throughout the autumn and winter of 1936. It must be borne in mind, however, that results obtained out of the normal season may embrace one or two possible sources of error. Thus, there is not sufficient knowledge available of the biology of the sheep fleece to enable us to say to what extent the amount and quality of secretions may vary, nor do we know how profoundly such potential changes may affect the larvae or the behaviour of introduced chemicals. Another possible source of error is that distinct variations may occur in the microclimate of the fleece at different seasons. Provided these qualifications are given due consideration, there is no reason why research on the maggot-fly problem should not proceed throughout the year.

SUMMARY

A method is described by which active cutaneous myiasis of sheep by *Lucilia sericata* larvae can be produced with certainty and precision at any season of the year. The method is such that it can readily be employed in field experiments.

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STUDIES IN AUSTRALIAN ACARINA LAELAPTIDAE

I. NEW RECORDS AND SPECIES OF *LAELAPS* AND ALLIED GENERA

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(With 5 Figures in the Text)

The material recorded and described in the present paper consists not only of the specimens in the South Australian Museum, but largely an immense number of specimens sent to the writer by Mr F. H. Taylor of the Department of Tropical Health, Sydney. To him, my best thanks are due for the opportunity to examine and describe this material. Types of the new species are in the South Australian Museum and paratypes amongst the material returned to the Department of Tropical Health, Sydney.

Genus **Laelaps** Koch. s.str.

Laelaps echidninus Berl.

Specimens of this common species are in the collections of the South Australian Museum from the following hosts and localities:

On rats, Sydney ,New South Wales, identified by Hirst (G. E. N., no date); on *Rattus norvegicus*, Adelaide, South Australia, 18 May 1936 (T. H. J.); on *Perameles gunni*, from between Portland and Hamilton, Victoria, 1936 (F. W. J.); on *Rattus rattus*, Cairns district, Queensland, 18 September 1936 (F. H. T.); on *Rattus rattus*, Ingham district, Queensland, no date (Drs J. and R.); on *Rattus culmorum*, Ingham district, Queensland, no date (Drs J. and R.).

Laelaps nuttali Hirst

(Fig. 1 *a–d*)

As the male sex of this species has not previously been described and figured, the following description and figures are given from specimens now in the South Australian Museum. The allotype male is from the following host and locality: *Rattus norvegicus* Townsville, Queensland, 23 September 1936 (S. Hirst).

Description of male. Size rather smaller than female, 465μ long by 290μ wide. Setae on both dorsum and venter, long (58μ) and slender, not excessively thick. First two pairs of legs slightly stouter than third and fourth, the second being rather stouter than first, coxae without distinct strong spines, but first to third with rather short setae about as strong as those on ventral shield,

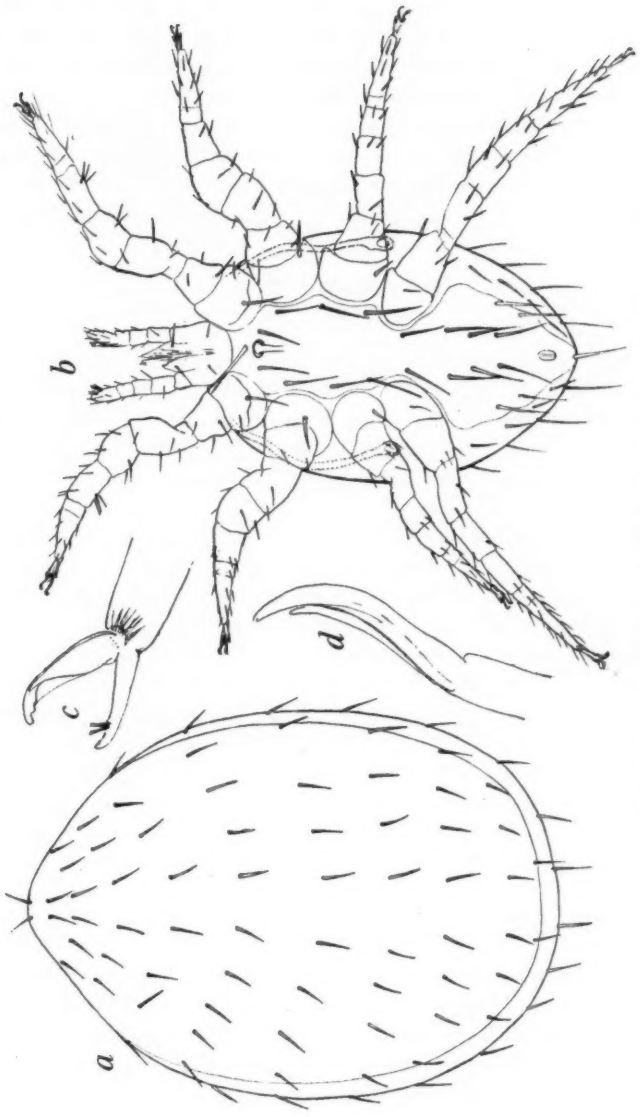

Fig. 1. *Laelaps nuttali* Hirst. *a*, dorsal view of female; *b*, ventral view of male; *c*, mandible of female; *d*, mandible of female.

setae on tarsi III-IV stronger than on I. All ventral shields united, furnished with eight medial pairs of long setae, one post-anal seta and two pairs of lateral setae on ventral portion of combined shield; outside of the ventral shield are four setae on each side. Junction of anal and ventral shields not demarcated.

The specimens in the South Australian Museum are from the following hosts and localities in addition to the allotype locality:

On *Rattus norvegicus* Cairns, Queensland, no date (F. H. T.); on *Perameles nasuta*, Ingham, Queensland, no date (A. H. B); on *Rattus culmorum*, Mackay, Queensland, no date (W. A. McD.); on *Rattus rattus*, Cairns district, 24 September 1936 (F. H. T.); on *Rattus culmorum*, Mackay, Queensland (W. A. McD.).

Laelaps hapaloti Hirst

(Fig. 2 *a–e*)

Hirst described this species from a series taken from a "jumping pouched marsupial mouse" (*Hapalotis*), collected by A. Rau, at Humbug Scrub, near Adelaide, South Australia. This type series is said to be in the South Australian Museum, but the writer has not been able to locate it. There is, however, another series from the same host species and locality collected by T. P. Bellchambers.

Exactly what the host was is very uncertain at the present time. Certainly it was not a species of *Hapalotis*, a name now sunk in favour of *Conilurus*, a genus of rodents, lacking any sort of pouch. According to Mr H. H. Finlayson, the host was probably a species of *Notomys*.

In the Museum collections are also specimens from a *Pseudomys* sp., from Wallara, Central Australia in 1932 collected by H. H. Finlayson.

Hirst's description of this species was published posthumously in 1931 (*Proc. Zool. Soc. Lond.*) and without figures, his drawings having been lost after his death. The following figures, therefore, are given from specimens of both sexes from the existent series from the type host and locality. There is little to be added to the original description, beyond stating that it is evidently only drawn from the female sex. A description of the male sex is therefore now given.

Description of male. Slightly smaller than the female, 1·26 mm. long by 0·83 mm. wide, quite as strongly chitinized as in female sex. Dorsal and ventral setae not exceptionally spine-like, rather slender, 116μ long. Legs fairly stout, coxae I and III with stout, short spinelets, that on II much longer but equally stout, setae on basal segments of legs fairly strong and stout, second basal segment of leg I (in both sexes) outwardly with a long seta much longer than body setae. All ventral shields united, but junction of anal and ventral shields well demarcated, combined shields with eight pairs of median long setae, one postanal setae, anal plate also with two small fine setae, the ventral part of combined shields not very wide and not taking up more than one-third of width of body, laterally the edges of this part have three setae on each side;

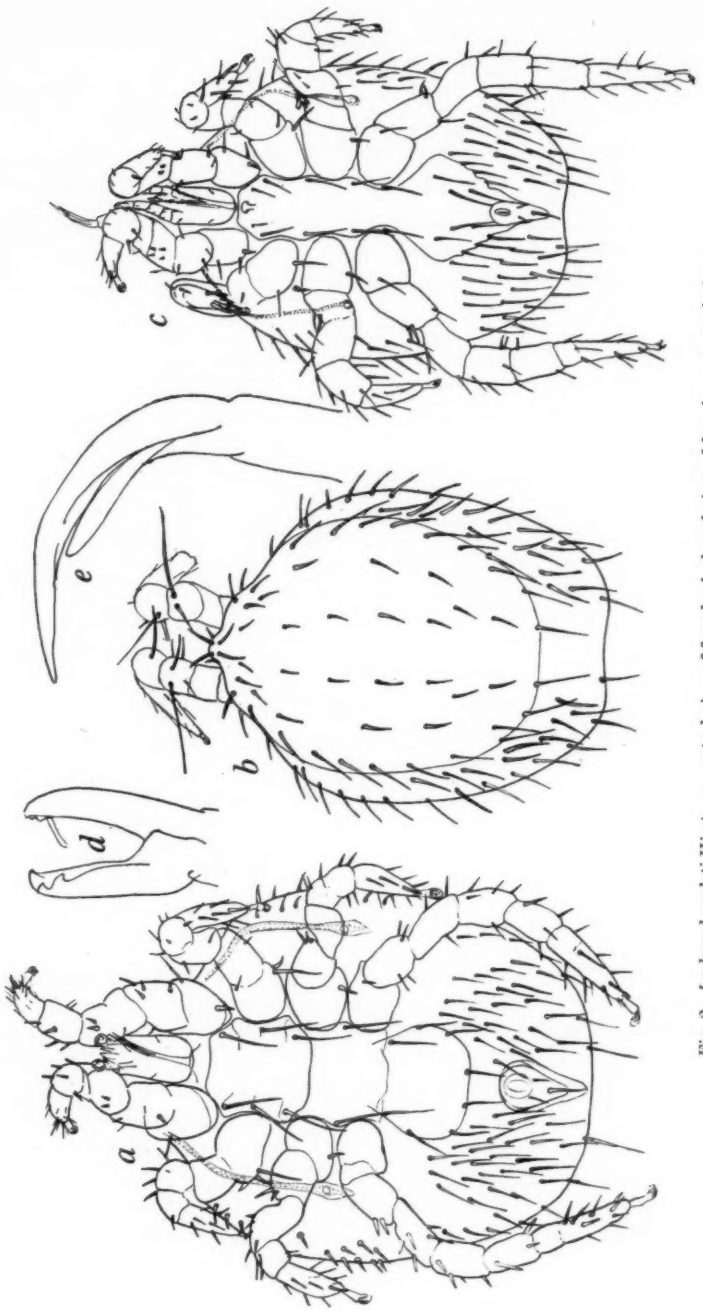

Fig. 2. *Laelaps hapaloti* Hirst. *a*, ventral view of female; *b*, dorsal view of female; *c*, ventral view of male; *d*, mandible of female; *e*, mandible of male.

on each side between the ventral shield and the edge of body are about seventeen setae. The posterior end of body is emarginate, and is not reached by the anal shield. Dorsal shield much as in female.

Laelaps melomys sp.n.

(Fig. 3 *a–b*)

This new species was taken on *Melomys littoralis*, in the Cairns district of Queensland from 6 to 17 September 1936 (F. H. T.) and again from as yet undetermined hosts,[1] from the same locality, 30 September to 5 October 1936 (F. H. T.)

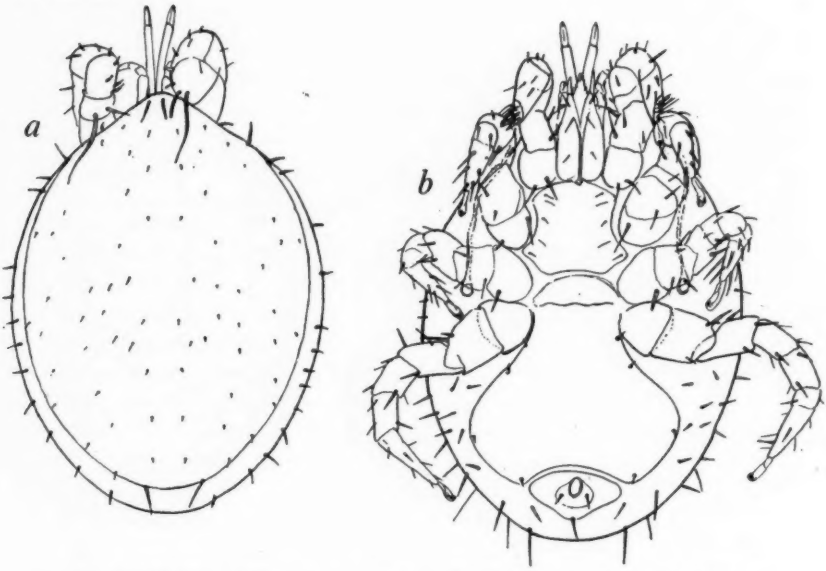

Fig. 3. *Laelaps melomys* sp.n. *a*, dorsal view of female; *b*, ventral view of female.

So far only the female sex is known. The species in its broad, posteriorly excavated ventral shield is closely related to *Laelaps echidninus* Berl., but differs in the wide anal shield, the short setae on the ventral shield, and the dorsal armature.

Description of female. Very dark and heavily chitinized species, 1·2 mm. long by 0·87 mm. wide. All ventral plates heavily chitinized, sternal plate about as broad as long with three pairs of short fine setae, posterior margin slightly concave, ventral plate very broad, more so than in *L. echidninus*, occupying about four-fifths of width of body, posterior edge concave and closely following anterior margin of anal shield, furnished with the usual four

[1] Now determined as *Melomys littoralis*.

pairs of setae but these exceptionally short, anal plate much wider than long with three setae, the postanal one being the longest; between the ventral shield and the body margin on each side are about eight short setae. Peritreme long and rather narrow, the spiracle lying opposite coxae III. The dorsal shield is large, leaving only a narrow outer margin, the capitulum with a pair of moderately long setae, and another pair at the apex of dorsal shield, otherwise this shield with 60–70 very short setae, outer dorsal margin with rather longer setae. Legs fairly stout with moderately stout spines, coxae II and III with a stout, fairly long setae, I with two such.

Laelaps finlaysoni sp.n.

(Fig. 4 *a–e*)

From *Pseudomys apodemoides* from Combe, South Australia, collected by H. H. Finlayson (Honorary Mammalogist, South Australian Museum) after whom the species is named; on *Pseudomys minnie*, Mulka, Lake Eyre, South Australia, no date (G. H.).

Description of female. Strongly chitinized, yellowish brown in colour, length 0·91 mm. long by 0·68 mm. wide, of very squarish form, with very definite shoulders. Dorsal shield fairly well chitinized, about three-fourths the body width, with many short setae, and two widely separated and longer ones at posterior margin, capitulum with a pair of strong setae, dorsal surface outside of shield without setae except at external edge. Legs fairly stout, anterior being rather stouter, coxae I with long seta and IV without spine-like setae, II with a pair of adjacent long setae, III with one shorter and stout seta; third segment of leg I with long outer seta. Ventral shields separated, sternal shield wider than long, posterior margin very slightly concave, with three pairs of fine short setae, ventral plate as figured with four pairs of setae, the posterior two pairs about 6–8 times as long anterior, anal plate as figured with three setae, between the anal plate and the margin there are two long setae, on each side and one or two short ones. Peritreme originating between legs III and IV. Legs with fine setae.

Male. All ventral shields united, combined shield with eight pairs of setae, all of which are long, except the fifth and sixth from front, which are short as in the female, anal shield demarcated with three setae, ventral portion of combined shield not very broad, about one-third body width, each lateral edge with two long setae. Legs I and II rather stouter than in female. Otherwise as in female, the male being remarkable for the much longer seta.

Laelaps muris Ljungh, 1799

Syn. *Laelaps agilis* Koch. 1836.

(Fig. 5 *a–c*)

Oudemans in his "Laelaps-Studien" (*Tijds. Ent.* **80**, 1927) refers Koch's species to a synonym of Ljungh's and gives some very excellent detailed figures of this species.

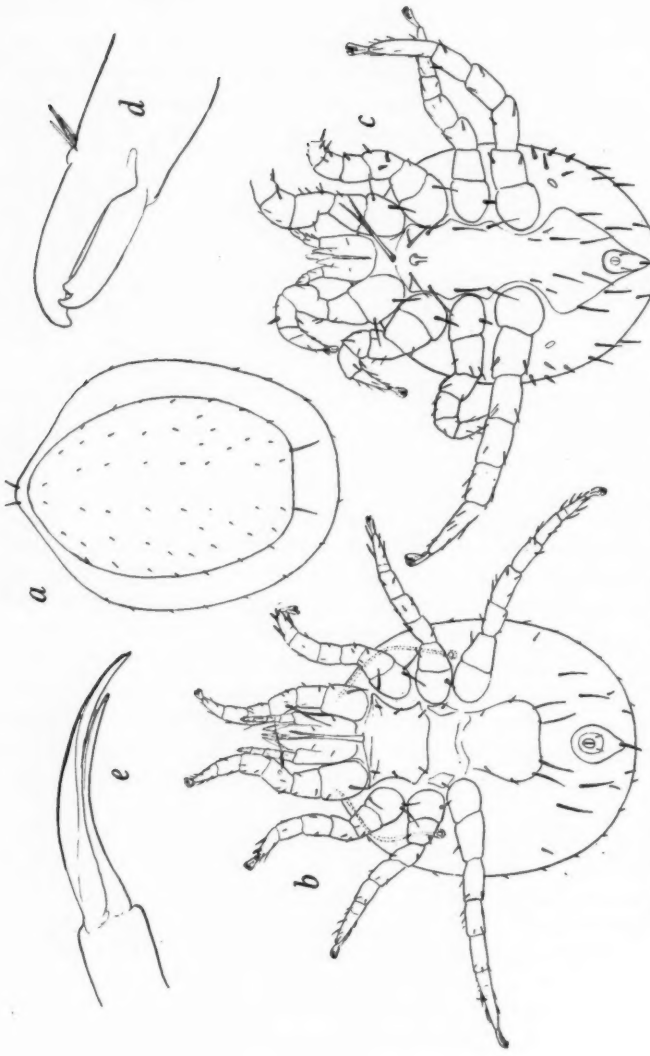

Fig. 4. *Laelaps finlaysoni* sp.n. *a*, dorsal view of female; *b*, ventral view of female; *c*, ventral view of male; *d*, mandible of female; *e*, mandible of female.

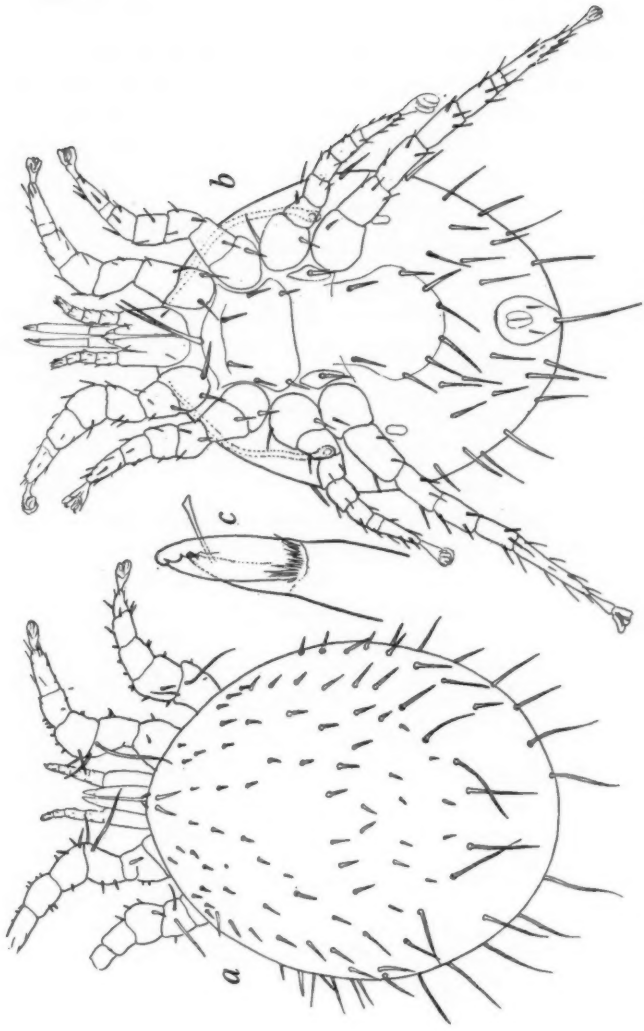

Fig. 5. *Laelaps muris* Ljungh. *a*, dorsal view of female; *b*, ventral view of female; *c*, mandible of female.

In the collections of the South Australian Museum is a slide of two female specimens taken from *Hydromys chrysogaster* at Adelaide, South Australia, by Prof. T. Harvey Johnston some years ago. The slide was presented to the Museum by Prof. Johnston.

An examination of these specimens reveals entire agreement with Fig. 15 of Oudemans' on p. 170, and they are therefore referred to the above European species. In case future study may reveal minute specific difference, however, figures drawn from the Australian specimens are given in this paper.

Genus **Heterolaelaps** Hirst

Heterolaelaps antipodianum Hirst

The Museum specimens are from the following:

On short-nosed bandicoot (*Isoodon obesulus*), Adelaide, South Australia, June 1934 (H. W.); on *Perameles gunni*, from between Portland and Hamilton, Victoria (F. W. J. 1936).

Genus **Mesolaelaps** Hirst

Mesolaelaps anomalus Hirst

From the following hosts and localities:

On *Perameles nasuta*, Townsville, Queensland, October 1935 (F. H. T.); on *Perameles macrurus*, Cairns district, Queensland, 17 September 1936 (F.H.T.).

Mesolaelaps australiensis Hirst

From the following hosts and localities:

On rats, Sydney, New South Wales (G. E. N.), no date, determined by Hirst; on *Rattus lutreola*, Lake Alexandrina, South Australia, May 1936; on *Perameles gunni*, between Portland and Hamilton, Victoria, 1936 (F. W. J.); on *Perameles macrura*, Ingham district, Queensland (Drs J. and R.), no date.

(*MS. received for publication* 18. I. 1937.—Ed.)

THE EGG-PARASITE OF *SIALIS LUTARIA*: A STUDY OF THE INFLUENCE OF THE HOST UPON A DIMORPHIC PARASITE

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From the Zoological Laboratory, Cambridge

(With 5 Text-figures)

Introduction

The occurrence of a trichogrammid egg-parasite of the alder-fly, *Sialis lutaria* Linn., was first recorded by Aurivillius (1898) and has since been mentioned by several students of the host, notably by Lestage (1919) and by Du Bois & Geigy (1935). The parasite was described by its discoverer under the name *Oophthora semblidis* (Aurivillius, 1898), but its identity has since been much confused. Silvestri (1908), for instance, has studied an egg-parasite of *Mamestra brassicae* under this name; while Kryger (1919) and Lestage (1921) call the *Sialis* parasite *Trichogramma evanescens*.

In his original description, Aurivillius reported two forms of the male of his new species. One form, which was common, was wingless. The other, which was very rare in his material, differed in being winged and in several other characters, particularly in the structure of the antennae. Neither Aurivillius nor any of the writers who have since mentioned it has offered any explanation of this dimorphism or even a clue to its source.

The present paper deals with the occurrence and prevalence of the parasite at Cambridge in 1936; and also, by providing a more complete description of the species than has been available, purports to settle the question of its identity. If that were all, however, the investigation would not now be added to an already overburdened literature. The real purpose of this paper is to describe a curious phenomenon observed while rearing the insect. It will be shown, in brief, that the appearance of one form or the other of the dimorphic male is dependent on the species of host in which the individual has developed. The effect of parasites upon their hosts has been the subject of many investigations. This paper reports an effect of the host upon its parasite.

Collection of the material

The flight of *Sialis lutaria* in 1936 began in Cambridge at about the beginning of May. On 6 May the eggs were already common on the leaves of *Glyceria aquatica* along the Granta, and with very little effort 46 egg-masses

were collected on that date. Collections were made thereafter at frequent intervals until 23 June, when only 4 egg-masses could be found in an hour. A thorough search on 1 July yielded none at all. The flight lasted, then, about 7 weeks. All the collections, which are listed in Table I, were made from one area—a small stream about 100 metres long at Coe Fen, Cambridge. The number of egg-masses collected on different dates in no way represents their relative abundance until 9 June. On that date and thereafter all those found in 1 hour of search were taken.

Table I. *Occurrence and emergence of* Sialis lutaria *and of its egg-parasite*

Lot	Date of collection	No. of egg-masses collected	Emergence of nymphs			No. of egg-masses parasitized	No. of parasites obtained
			Complete	Partial	None		
A	6 May	46	44	2	0	1	102
B	8 „	30	28	1	1	—	—
C	11 „	62	52	6	4	—	—
D	20 „	20	15	2	3	3	208
E	27 „	20	19	0	1	—	—
F	30 „	10	10	0	0	—	—
G	2 June	10	9	0	1	—	—
H	5 „	20	16	4	0	3	133
J	9 „	101	85	11	5	8	523
K	16 „	64	56	5	3	1	96
L	23 „	3	1	2	0	3	275
Total		386	335	33	18	19	1337

Table II. *Size of egg-masses and emergence of nymphs of* Sialis lutaria

Collection of 6 May				Collection of 9 June			
Egg-mass	No. of nymphs emerged	No. of eggs shrivelled	Total no. of eggs in mass	Egg-mass	No. of nymphs emerged	No. of eggs shrivelled	Total no. of eggs in mass
1	675	3	678	1	316	16	332
2	643	53	696	2	323	22	345
3	703	5	708	3	441	14	455
4	703	7	710	4	444	20	464
5	704	11	715	5	460	12	472
6	721	5	726	6	557	26	583
7	739	2	741	7	597	12	609
8	740	3	743	8	583	48	631
9	735	10	745	9	691	15	706
10	732	31	763	10	724	20	744
Total	7095	130	7225	Total	5136	205	5341
Average	710	13	723	Average	514	21	534

Oviposition by *Sialis* has recently been studied by Du Bois & Geigy (1935), to whom reference should be made for a full account of the process and a description of the egg. Here we are concerned principally with numbers. The eggs in 10 masses collected on 6 May were counted in full, with the results shown in Table II. There was an average of 723 eggs per mass. The size of the masses decreased as the season went on, and 10 collected on 9 June, also listed in Table II, contained an average of only 534 eggs. Assuming a mean throughout the season of about 600 eggs per mass, the collections made in the present survey included nearly a quarter of a million eggs.

The viability of the eggs under laboratory conditions was very high. The

20 masses listed in Table II gave an emergence of 98 per cent of the nymphs from the earlier collection and 95 per cent from the later. Out of the total of 386 egg-masses collected, 335 gave a similar complete emergence (95 per cent or more); 33 a partial emergence; and 18 masses gave no nymphs at all. Judging from the few empty egg-masses found in the open, natural emergence is not less than this. It is clear that there is little "intrinsic mortality" of *Sialis* eggs.

The trichogrammid parasite that is the subject of this paper occurred in one egg-mass of the 46 collected on 6 May. It appeared next in 3 of the 20 masses collected on 20 May. Then, after a second interval of 2 weeks, it emerged from a few egg-masses of each lot collected after 2 June. At the temperature that prevails during May, the life cycle of the parasite is in the order of 15 days, so that it would be reasonable to consider the emergents of 6 May, of 20 May, and of June as representing three successive generations of the parasite. Since *Sialis* eggs are available for only a few weeks, the parasite must live for the rest of the year at the expense of other hosts; but from what host it comes to attack the *Sialis* eggs and into what host it goes when the season for *Sialis* is over is quite unknown.

Of the total of 386 egg-masses collected, 19 were found to have been attacked by this parasite. The number of individuals emerging from an egg-mass ranged from 2 to 231, with an average of 70. The general parasitism of the whole collection, then, again assuming an average of 600 eggs per mass, was in the order of 0·6 per cent. In all, 1337 individuals of the parasite were obtained from the collected *Sialis* eggs; 239 of them males and 1098 females. The point to be especially noticed is that every one of these males was of the wingless form.

It was an obvious procedure, when the parasite had been obtained in the field, to attempt to rear it in the laboratory on the same hosts as are used for *Trichogramma evanescens*. Accordingly, healthy eggs of *Ephestia kuehniella* were exposed to female emergents. They were readily attacked, turned black in due course, and on the 10th day (at 25° C.) yielded 534 parasites of the first filial generation, of which 184 were males and 350 were females.

These progeny caused great astonishment. The females were in all respects like their mothers reared from eggs of *Sialis*; but the males were very unlike their fathers. Instead of being wingless, these males were all fully winged.

Two questions immediately arise. First, is the male really dimorphic, or are the wingless males merely imperfectly developed individuals such as may be produced in *Trichogramma evanescens* by starvation? Secondly, if the male is really dimorphic, what factors control the appearance of one form or the other? These questions are dealt with in the two following sections of the paper.

THE FORMS OF THE PARASITE

The description and figures published by Aurivillius are excellent, and in most respects correctly and sufficiently represent the *Sialis* parasite. In the following paragraphs, therefore, attention is largely confined to characters

which are of use either to distinguish the two forms of the male sex, or to establish the validity of the species as distinct from *Trichogramma evanescens*.

Females reared from *Sialis* average 0·54 mm. in length. In colour they are grey-brown with dark red eyes. The antennae (Fig. 1*a*) are composed of six distinct segments. On each funicle segment and at the base of the club is a minute structure composed of a knob on the end of a short stalk. The club is

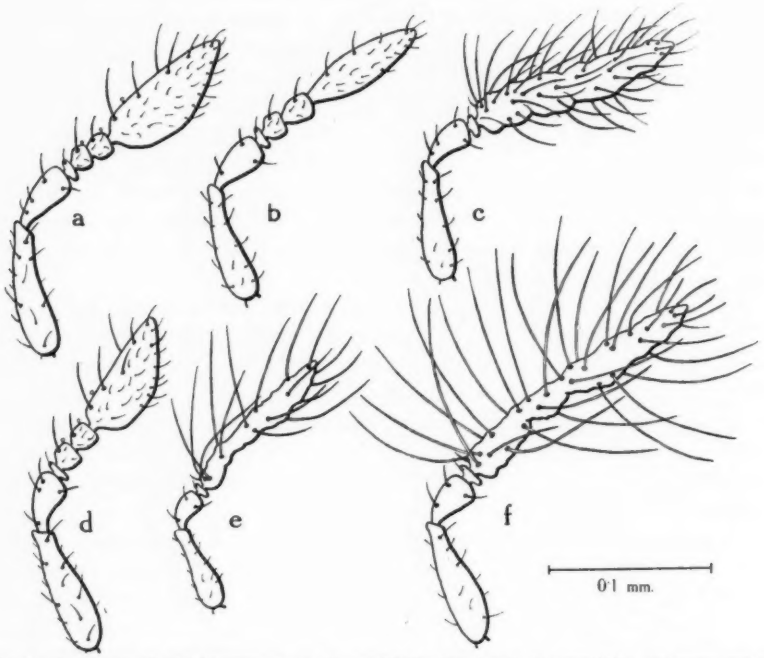

Fig. 1. Antennae of *Trichogramma*. *a*, *T. semblidis*, female; *b*, *T. semblidis*, apterous male; *c*, *T. semblidis*, winged male; *d*, *T. evanescens*, female; *e*, *T. evanescens*, male runt; *f*, *T. evanescens*, male.

much swollen. Mature females are always fully winged; the wings slightly fuscate at the base. The legs are pale amber-coloured and slender, the tarsal segments, in particular, all more than twice as long as broad.

Their daughters, reared on *Ephestia kuehniella*, and their female descendants reared for 20 generations on *Sitotroga cerealella*, do not differ in any respect except that of size.

Winged males (Fig. 2*a*), the sons of the females described above, average 0·47 mm. in length when reared on *Ephestia kuehniella*. When they emerge from the host their wings, like those of the females, are developed but not expanded, and it takes an hour or two for them to extend and dry. In colour, these males are similar to the females. The two funicular segments of the

antenna (Fig. 1*c*) are not separated from the club, with which they seem to form one long segment about five times as long as its average width. This compound club bears about 40 long setae which give the antenna a plumose appearance. It is to be noticed that these setae are in no case as long as the scape. The legs (Fig. 3) are slender; the tarsi in particular being more than

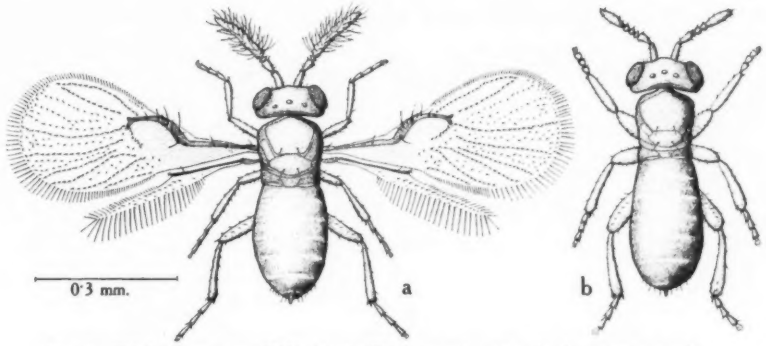

Fig. 2. *Trichogramma semblidis* (Aurivillius). *a*, winged male; *b*, apterous male.

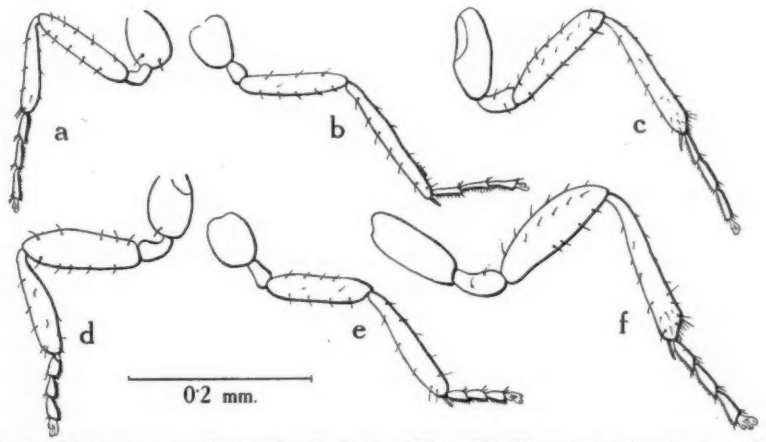

Fig. 3. *Trichogramma semblidis*. *a*, *b* and *c*, front, middle and hind legs of winged male; *d*, *e* and *f*, same of apterous male.

twice as long as wide, as in the female. Cleared specimens of females and winged males reveal an enormous development of the postphragma (Fig. 4) which seems quite out of proportion to the size of the insect or the strength of its flight.

Apterous males (Fig. 2*b*), reared from *Sialis* eggs collected in the field, measure 0·55 mm. in length. They are rather darker in colour than the winged males. At low magnifications they appear completely wingless, and only by

careful examination under high power is it possible to see two minute lobes on each side which may represent wings. These lobes, it is to be emphasized, are extremely small, and quite different from the unexpanded wings of newly emerged females or winged males. The antennae (Fig. 1*b*) are composed of six distinct segments; the two funicle segments being not at all fused with the club. The club is not grossly swollen, as it is in the female; and lacks the numerous long setae which adorn the compound club of the winged male. The legs (Fig. 3) are stoutly built, the front legs appearing almost awkward in their strength. The tarsal segments, in particular, are short and broad. Apterous males entirely lack the posterior prolongation of the postphragma.

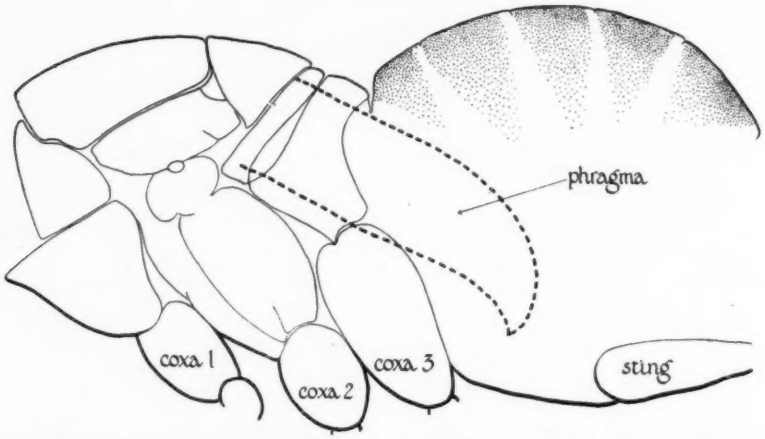

Fig. 4. *Trichogramma semblidis*, female. Side view of thorax and part of abdomen of cleared specimen, showing the great development of the postphragma.

The first matter to be disposed of is the possibility, mooted by Lestage (1919), that the apterous males described above are imperfectly developed specimens. It is well known that in *Trichogramma evanescens* there sometimes occur individuals which appear to be brachypterous or even wingless and which have been described by some authors as an apterous form. Zulueta (1928) and Salt (1936), however, have shown that these are merely starved individuals which emerge when a host has been superparasitized. They are much smaller than normal specimens, a fact recorded by writers who nevertheless describe them as a distinct apterous form. They are not always, indeed, entirely apterous, but usually bear partially developed wing pads which they are too feeble to expand. Their antennae (Fig. 1*e*) are typically male in structure, though reduced in size and with comparatively few long hairs. Salt (1936) has referred to them as "walkers" but, since that term is used by Graham-Smith (1916) in a different sense, would prefer to substitute the word "runt" (*O.E.D.* a stunted or undersized individual).

The apterous males of the *Sialis* parasite are not runts produced by starva-

tion. First, they are of large size. Their average body length is equal to that of the females with which they occur, and even greater than that of the winged males reared on *Ephestia*. Next, they are constant in occurrence. All of the 239 males that emerged from *Sialis* eggs collected in the field were of this form. Thirdly, their structure is not merely an imperfect or immature copy of the winged form, but is totally different in several characters listed below. Finally, there are no intermediates. All of the mature males examined clearly belong to one form or the other.

The winged and apterous males of the *Sialis* parasite, then, are to be considered two distinct forms of equal rank. They differ most obviously in the presence and absence of wings. The antennae are plumose in the winged male; without long hairs and quite different in structure in the wingless male. The legs are slender in the former; stout and of different proportions in the latter. The conspicuous postphragma of the winged male is lacking in the apterous form. It is clear, in short, that in this species there is a true and fundamental dimorphism of the male sex.

The question of the identity of the parasite has next to be considered. There can be no doubt that the species under discussion is that described by Aurivillius (1898) as *Oophthora semblidis*. Its structure agrees in every particular with Aurivillius's figures and description, and it was obtained from the same natural host. It would be sufficient for our main purpose, therefore, simply to call the parasite by that name. Since, however, several authors have considered the *O. semblidis* of Aurivillius to be the same as *Trichogramma evanescens* Westwood, and since a strain of the latter species is available for comparison, it will be useful to systematists to indicate characters in which the two species differ.

The specimens used for comparison with the *Sialis* parasite are from a strain reared for many years in the laboratory and of which the origin has already been briefly mentioned (Salt, 1935). Specimens of this strain were determined by the late J. Waterston of the British Museum as *Trichogramma evanescens* Westwood; and under that name members of the strain have been studied by Hase and his students; have been the subject of several papers by the present writer; and have been distributed to several parts of the world by the Imperial Institute of Entomology. The insects agree with Westwood's original description (1833) as amended (1879) in the matter of the antennae. It is a very likely assumption, then, that the specimens used for comparison do indeed represent the species *T. evanescens*.

Granting that assumption, the *Sialis* parasite, *Oophthora semblidis*, is not the same as *Trichogramma evanescens*. The most striking difference is found in the antennae of the males (Fig. 1*c* and *f*). The compound club of the *Sialis* parasite is about five times as long as its average diameter; that of *Trichogramma evanescens* is much more slender, being about eight times as long as broad. A curious plate or scale at the basal angle of the compound club of *semblidis* is quite lacking in *evanescens*. Perhaps the most easily observed

difference, however, is in the length of the setae on the club, which are only about half as long in the *Sialis* parasite as in *Trichogramma evanescens*, being not so long as the scape in the former and much longer than the scape in the latter species. No satisfactory character for distinguishing the females has been found, although a difference in the shape of the pedicel and the arrangement of the four setae on it (Fig. 1*a* and *d*) holds for many specimens. Colour provides an unsatisfactory character: living females of the *Sialis* parasite are rather uniformly grey-brown, while those of *Trichogramma evanescens* have a yellowish head and thorax and a dark abdomen.

To settle the matter in biological fashion, 6 virgin males and 9 virgin females of each species were obtained by isolating their hosts. The 6 males of each species were then placed in a small vial with the 9 females of the other. The males exhibited less excitement than when confined with females of their own species; nevertheless several attempts at copulation and some apparently complete acts of copulation were observed in each vial. After an hour, the two groups of 15 parasites were placed in two dishes with an adequate supply of healthy *Sitotroga* eggs. Both species are, of course, capable of arrhenotokous parthenogenesis, and the females began at once to attack the hosts provided. Of the females of *semblidis* there were 87 progeny, all males and all typically *semblidis*. Of the females of *evanescens* there were 159 progeny, again all males, and all typically *evanescens*. No female progeny, which develop only from fertilized eggs, appeared. It is clear, then, that although the two species may attempt to interbreed, they are incapable of actually doing so.

Further differences of physiology and behaviour will be described in a later paper. Enough has been said to demonstrate that the parasite of *Sialis* is at least specifically distinct from *Trichogramma evanescens*.

The genus *Oophthora*, on the other hand, is probably synonymous with *Trichogramma*. The character on which it was separated by Aurivillius, the relative lengths of the thorax and abdomen, is not very satisfactory, for the abdomen is longer than the thorax in both cases. Aurivillius may have been misled by Westwood's description, which appears to have been drawn up from dried specimens in which the abdomen had shrunk. In any case, the character is scarcely of generic value. Females of *evanescens* and *semblidis*, the type species of the two genera, are not distinguishable with certainty by any character yet discussed. Several systematists have already considered the two genera synonymous. In brief, the genus *Oophthora* of Aurivillius is probably not valid, although his species, *semblidis*, is good. The parasite of *Sialis* eggs is, therefore, to be called *Trichogramma semblidis*.

The influence of the host on the parasite

It has been shown that the male sex of the *Sialis* parasite, *Trichogramma semblidis*, is truly dimorphic. It remains in this section to investigate the factors that control the occurrence of the two forms.

For this purpose the parasite was reared on four species of hosts. Three of

them, *Ephestia kuehniella*, *Sitotroga cerealella*, and *Barathra brassicae*, were moths of which a constant supply of healthy eggs was available from cultures kept in the laboratory. The fourth was the original host, *Sialis lutaria*, which readily oviposited in captivity and so provided unparasitized eggs for experiment. Glass vials, 40 mm. long and 12 mm. in diameter and closed by corks, were used as containers. They were fitted with a piece of stiff paper, 30 mm. long and 10 mm. wide, on which the hosts, a single egg-mass in the case of *Sialis*, a group of about 100 eggs in the case of the moths, were gummed. Only one female parasite was put into each vial, so that the emergents in any vial were always of one family.

The following example shows the method used. An egg-mass of *Sialis* collected on 20 May yielded 3 male and 53 female parasites; the males, of course, of the apterous form. One of the females was put into a vial containing eggs of *Ephestia*. A total of 57 progeny emerged, 7 males and 50 females. The males were all of the winged form. Two females of this family, being sisters fertilized by their brothers, were put into two separate vials, one containing eggs of *Ephestia*, the other eggs of *Sialis*. The one placed with *Ephestia* eggs had 35 progeny, 6 males and 29 females. The males were all of the winged form. The one placed with eggs of *Sialis* had 51 progeny, 10 males and 41 females. The males were all of the apterous form. From the 29 females emerged from eggs of *Ephestia*, again for the second time sisters fertilized by their brothers, three were placed in three separate vials, one containing eggs of *Ephestia*, another eggs of *Sitotroga*, and the third eggs of *Sialis*. In the first vial emerged 4 males and 27 females, the males all winged; in the second 9 males and 37 females, the males all winged; in the third 4 males and 18 females, the males all apterous.

The foregoing example indicates the method used, and it will suffice now to give the results of the whole series of rearings. This is most clearly and briefly done by means of the diagram (Fig. 5).

As the figure shows, fairly full and representative rearings were carried to the third filial generation. Then, the season being over, the supply of *Sialis* eggs ran out. The strain was, however, preserved. The family reared on eggs of *Sitotroga* in the example cited above was continued on that host and at the time of writing is in its 20th generation. The very different sex ratios recorded in the diagram are not significant, since in many cases unfertilized females were used deliberately in order to increase the number of male progeny.

It will be observed at once that both winged and apterous males appeared in each filial generation. Therefore, no hypothesis of a regular alternation of generations will serve to explain the occurrence of the two forms. Nor can the dimorphism be spurious and due to the segregation of two distinct species from the original *Sialis* eggs, because the pure lines, of which one has been described in detail above, show no correlation at all between the form of a male and that of its nearest male relative, its uncle or its maternal grandfather. Physical factors of the environment cannot explain the result for, although the

parental generation was exposed to the fluctuating temperatures of an English May, all the following generations were reared under the same conditions of temperature, humidity, and light.

The only correlation to be found, and it is an extremly close one, is that between the form of the male parasite and the kind of host from which it emerged. In the whole series of rearings there were 277 male emergents from eggs of *Ephestia*; 33 males from eggs of *Barathra*; and 28 males from eggs of *Sitotroga*. All of these 338 males reared on moth eggs were of the winged form. From *Sialis* eggs collected in the field there emerged 239 males, and from *Sialis*

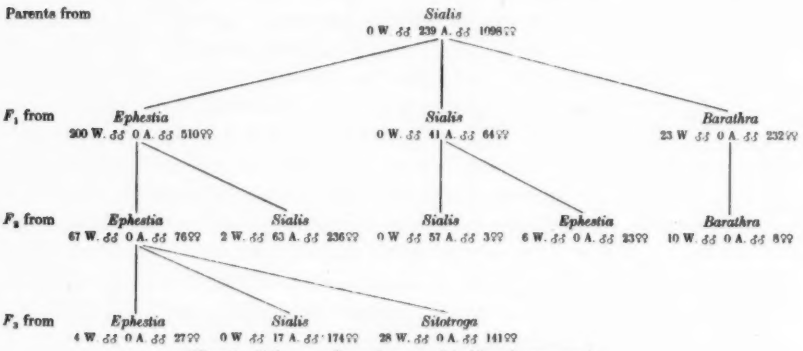

Fig. 5. Scheme of rearings and table of emergents.

eggs laid and parasitized in the laboratory 180 males. Of these 419 males reared on *Sialis* eggs, 417 were of the apterous and only 2 of the winged form. In 755 cases out of 757, then, the form of the male was exactly correlated with the kind of host from which it emerged. Winged males came from the lepidopterous hosts, apterous males from the eggs of *Sialis*.

There were two exceptions. These are not a mistake, for the two winged males were observed among their apterous brothers before the vials were opened. There was no other host present, and the two must have emerged from *Sialis* eggs. No explanation can be offered. But the disagreement of only two cases out of 757, while it invites further investigation, must not prevent the drawing of a reasonable conclusion.

The results of this investigation show clearly that in the case of the dimorphic males of *Trichogramma semblidis* it is the host that principally determines which form of the parasite shall emerge.

Discussion

Four collections of the *Sialis* egg-parasite have previously been recorded. Aurivillius (1898) found his type series at Blidö, Sweden; Kryger (1919) obtained his material from several localities in Denmark; Lestage (1919) received his specimens from Rouge Cloître, Belgium; and Du Bois & Geigy

(1935) found the parasite at the Sempachersee and at Basle, Switzerland. No numbers are given by any of these writers, but Lestage and Du Bois & Geigy imply that the incidence of the parasite was low in their collections, as it was in the present case; while Aurivillius, who collected the *Sialis* eggs in order to rear the nymphs, says that "almost exclusively" parasites emerged.

A more important difference to be noted in these collections is in the occurrence of the two forms of the male. Aurivillius reared both forms from the *Sialis* eggs he collected, but the winged form was "extremely rare". Lestage says that in his material "les ♂ aptères me paraissent au contraire plus rares". Kryger records 315 females, 324 apterous males, and no winged males as having emerged from a collection of *Sialis* eggs, but it is not clear from his account whether he ever reared the winged male from that host. He obtained winged *Trichogramma* males from lepidopterous hosts collected in the field but, since he did not distinguish between *semblidis* and *evanescens*, it is not certain that these were not the latter species. Du Bois & Geigy found only the apterous males. The experience of Aurivillius, of Kryger, and of Du Bois & Geigy, then, is similar to that of the present writer. Lestage's observation alone is discordant. No explanation can be offered, but it may be pointed out that he was not aware of the difference between *T. semblidis* and *T. evanescens* and that, since he did not collect or rear the material himself, there may have been contamination.

Another matter to do with the incidence of the parasite is the question of its hosts before and after the flight of *Sialis*. One would like to know in what host it overwinters, and whence it emerges so early to attack the first *Sialis* eggs. It is probable that during the summer *Trichogramma semblidis* occurs in a variety of hosts which induce the winged male with plumose antennae; and it may well be that on this account the parasite has been determined, when it was found, as *T. evanescens*.

The demonstration given above of the specific distinctness of *T. semblidis* and *T. evanescens* allows one or two points of confusion in the literature to be cleared up. Gatenby (1917) describes the embryology of a parasite which he calls *T. evanescens* obtained from eggs which he says are those of *Donacia simplex*, a Chrysomelid beetle. His description and figure make it certain that the hosts were not the eggs of *Donacia* at all, but eggs of *Sialis*. It is highly probable, therefore, that Gatenby's paper describes the embryology of *Trichogramma semblidis*.

Embryologists need not fear, however, that they are without a study of *T. evanescens*. The embryology of a parasite called *Oophthora semblidis*, obtained from eggs of *Mamestra brassicae*, was studied by Silvestri (1908). The same material was described from a systematic point of view by Masi (1909). It is very likely that these authors were in fact dealing with *Trichogramma evanescens*, for four reasons: (1) The host, *Mamestra brassicae*, is a common host of that species. (2) The so-called apterous males of these authors were only about half the size of the winged males; that is, were probably runts.

(3) The material included intermediates of moderate size with rudimentary wings. (4) The so-called apterous males had antennae like the winged males.[1]

In view of the confusion of the two species that has prevailed, other records of the collection of *Oophthora semblidis*, for instance those of Marchal & Feytaud (1911), are to be accepted with caution.

The principal problem dealt with in the present paper is that of the occurrence and control of the dimorphism of the male *Trichogramma semblidis*. That a chalcid should occur in two forms occasions no great surprise, for the Hymenoptera seem particularly prone to dimorphism; but that the appearance of one form or the other should be amenable to experimental control is a matter of some interest. It will be worth while, therefore, first to review briefly some of the other cases of dimorphism found in the Hymenoptera, and afterwards to consider whether any of them are determined in a manner analogous to that described above for the parasite of *Sialis*.

Dimorphism in the Hymenoptera is of several types. It reaches its highest development in the social groups where the females are usually dimorphic (bees and wasps) and often polymorphic (ants). In the Cynipidae, where the difference between two forms of the same species is sometimes so profound that they have been put into different genera, it takes the form of a regular alternation of generations, usually of sexual and agamic individuals attacking different parts of the host plant (Kinsey, 1920, p. 372).

Among the parasitic Hymenoptera, dimorphism most frequently consists of alternative winged and apterous or subapterous forms. In *Pezomachus flavocinctus* (Strickland, 1912) and *P. sericeus* (Thompson, 1923) the male occurs in winged and apterous phases; in *Harmolita grandis* (Phillips & Poos, 1923) and *Hemiteles hemipterus* (Salt, 1931) it is the female that is dimorphic; while in *Sycosoter lavagnei* (Lichtenstein & Picard, 1917) and *Scleroderma immigrans* (Bridwell, 1920) winged and apterous individuals of both sexes are found. In all of these cases the winged and apterous individuals are identical in other morphological characters. They differ only in the development of the wings, and to some extent in size, since in general the winged specimens are larger.

In a few other cases, for instance *Melittobia acasta* (Picard, 1923) and especially *Philotrypesis* (Grandi, 1921), the males occur in a series of forms which show progressive degeneration of the wings and other appendages with decreasing size. These males have been called polymorphic, but to use the term for such cases is to debase it. Polymorphism properly refers to a number of distinct forms. The forms in these cases are not distinct since they intergrade continuously throughout their range and differ only quantitatively, not in character.

The dimorphism of *Trichogramma semblidis* is unlike any of the cases yet described in the parasitic Hymenoptera. It is precise: the two forms are not

[1] "Le antenne dei maschi alati e di quelli atteri differiscono pure per la loro lunghezza e per il numero, forma, e disposizione delle setole" (Silvestri, 1908, p. 72).

connected by intermediates and differ in kind not only in degree. It is fundamental: not merely the wings but also other parts of the body are radically altered. In both of these respects the dimorphism under discussion most nearly resembles that of the Cynipidae and the social Hymenoptera; but in those cases it is the female that is dimorphic, here it is the male.

Diverse as are the phenotypes of dimorphism in the Hymenoptera, one causal factor seems to be common to them all. That is the factor of nutrition. In the case of the social Hymenoptera, the influence of food upon a labile plasma has long been invoked as at least the elicitor of dimorphism. The most recent view (Wheeler, 1928) seems to be that some, if not all, of the normal castes of ants are produced by peculiarities of feeding. In wasps and in *Bombus*, the tiny spring workers are almost certainly the result of undernourishment, while in *Apis* it has been shown beyond dispute that it is a difference in food that produces either a queen or a worker from a female egg. It is significant that the alternating forms of the Cynipidae develop under quite different trophic conditions, in dissimilar galls on different parts of the food plant. It would be interesting to try to upset the regular alternation of generations of gall wasps by experimental transplantation of the cynipid egg from one site to the other.

In the parasitic Hymenoptera, too, dimorphism probably has a nutritional basis. Strickland (1912, p. 131) says that in *Pezomachus flavocinctus* the apterous males "are much smaller than the winged forms which would suggest that their apterous condition is in some way connected with an insufficiency of food". Thompson (1923) reared two male progeny of one female of *P. sericeus*; one on a large host, the other on a small host. The male that emerged from the former was large and fully winged, that which came from the small host was tiny and completely apterous. In *Harmolita grandis* (Phillips & Poos, 1923) the winged summer form is much larger and more robust than the apterous spring form. Lichtenstein & Picard (1917, p. 457) say that in *Sycosoter lavagnei* "les ailés sont d'une taille supérieure à celle des aptères. On pourrait donc admettre qu'une nutrition insuffisante en réduisant la taille de l'adulte, agit aussi en entravant le développement des disques alaires."

A difference in either quantity or quality of food seems effective to elicit dimorphism. Certainly in *Apis* it is the change in diet on the third day of larval life that leads to the development of a worker from a female egg; while in *Bombus* and the social wasps it is the *amount* of nourishment supplied that seems to be the effective agent. Whether it is the kind or the quantity of food that usually operates in the parasitic Hymenoptera is not clear; in the cases cited above, the food of the related forms seems to differ more significantly in mass than in character, but experimental evidence on the point is lacking.

There can be little doubt that the dimorphism of *Trichogramma semblidis* is controlled by nourishment, and by a difference in its kind rather than in its amount. The four hosts used in this investigation are of different sizes and therefore provide the parasite with different amounts of food. *Sitotroga* is the

smallest, *Ephestia* is next, *Sialis* is still larger, and *Barathra* is the largest. The parasites that emerge from these four hosts vary in size with the host from which they come. But it is not the smaller hosts that produce apterous males and the larger that produce the winged form. The winged males that emerge from *Sitotroga* and *Ephestia* are smaller, while winged males from *Barathra* are larger, than the apterous males from *Sialis*. It seems clear that in this case it is not the amount of food that matters. There remains only the difference in the kind of food provided by the hosts to explain the appearance of the two forms.

It emerges from the foregoing discussion that the dimorphism of *Trichogramma semblidis* is especially interesting in the following respects: (1) The alternative forms differ more fundamentally than those of any other example yet described in the parasitic Hymenoptera. (2) For the first time, the dimorphism of a Hymenopterous parasite is shown to be controlled by the species of host on which it develops. The case therefore provides a striking example of the influence of a host upon its parasite. (3) *Apis mellifica* and *Trichogramma semblidis* furnish the only two examples of dimorphism in the Hymenoptera that have yet been made subject to experimental control. In both cases the alternative forms are elicited by differences in the kind of nourishment consumed during their development.

Summary

1. Nearly a quarter of a million eggs of *Sialis lutaria* were collected at Cambridge in 1936. About 0·6 per cent of them were attacked by a parasite.

2. The egg-parasite of *Sialis* is distinct from *Trichogramma evanescens*, and is to be called *T. semblidis* (Aurivillius).

3. The male of *Trichogramma semblidis* occurs in two forms. Neither consists merely of imperfect or degenerate individuals of the other, for the two forms are equally large and differ constantly and fundamentally in several characters. The species, therefore, exhibits true dimorphism.

4. Rearing experiments involving isolated pure lines show that it is principally the host that determines which form of the parasite shall emerge. Males reared on *Sialis* are of the apterous form; those reared on three species of Lepidoptera are of the winged form.

5. The dimorphism of *T. semblidis* is discussed in relation to other examples of dimorphism in the Hymenoptera. It is shown to have several features of special interest.

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NOTE ON APSTEIN'S PARASITES AND SOME VERY EARLY LARVAL PLATYHELMINTHES

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(With 2 Figures in the Text)

The paper by Apstein (1911) is the only previous work known to me which is concerned with parasites of marine pelagic Crustacea in general, chiefly Copepoda, and especially of *Calanus finmarchicus*. It is of the nature of a preliminary note, since his work in the neighbourhood of Kiel was suddenly interrupted in its early stages; so that, while some of his "parasites" are easily identifiable, the scanty notes on others are difficult of interpretation and have given much trouble to subsequent writers. After making observations on the parasites of *Calanus* in the Clyde Sea Area[1] over a period of several years, I feel in a position to offer the following opinions on Apstein's note together with an account of very early stages in the development of some larval Platyhelminthes.

Parasite 1. This is clearly one or more species of *Blastodinium*. Chatton (1920), who criticizes Apstein's work very severely (p. 200), identifies it as *B. hyalinum*. He makes no comment on the fact that Apstein found "hier und wieder" two, three and once five parasites in one stomach, while Chatton himself describes the species as typically solitary in the Mediterranean.

Parasite 2. I have seen nothing which gives any clue as to what these objects may have been.

Parasite 3. This heading includes a number of Gregarines. Of these No. 3 *a*, from *Calanus*, with its 20μ nucleus, and No. 3 *d*, from *Mysis*, with its septum, seem to be different; but as far as Apstein's description goes, No. 3 *b*, from *Calanus*, and also perhaps No. 3 *c*, from *Temora*, might well be the same as the Gregarines I have described in the Clyde *Calanus* (Jepps, 1937). No dimensions are given, and the figures are evidently made from hasty sketches so that too much importance should not be attached to small discrepancies between them and mine, some of which are also taken from rough notes.

Parasite 4 might very well be a stage, perhaps degenerate, in the sporulation of one of the plasmodial parasites of the body cavity. If it were *Paradinium* it would represent a frustrated sporulation which has been seen to give rise to bodies like those here described (see Jepps, 1937).

Parasite 5 cannot be identified from my experience. Again no size is given which adds to the difficulty.

Parasites 6–8. I am in agreement with Apstein that these are all stages of the same type of parasite, even though they may not belong to the same

[1] See Nicholls, A. G. (1933), *J. Mar. biol. Ass. U.K.* **19**, 85, for map of this area.

species. I had diagnosed similar structures in my material quite differently, making the same erroneous guess that parasite 6 might be a young *Ichthyosporidium* as is given by Apstein on p. 15, and including with it parasite 7 (cf. Chatton, 1920, p. 287). A further study of two of these cases of "Ichthyosporidium" showed my mistake. One infected female *Calanus* with "isolated pieces"[1] and "spheres"[1] of parasite was kept alive in the hope of seeing further development; two days later it was found that the parasite had increased in amount, and besides the main concentration in a bunch near the stomach (cf. Fig. 1 A) was scattered through the cephalothorax. (Later some of the smaller pieces were being carried round in the circulation. It would be interesting to know whether this is normal and accounts for the spreading of the parasite throughout the *Calanus*.) To my surprise, although it showed no structural differentiation it was now "writhing about" in a manner much more worm-like than protistan. (Apstein refers to the movements of extension and contraction of his parasite 6.) Outlines of some of the pieces are shown in Fig. 1 B, and these were seen to be "full of vesicular nuclei of varying size". The *Calanus* died after 8 days in the laboratory before any differentiation could be seen in the parasite. The other infected *Calanus*, sketched in Fig. 1 A, may be compared with Chatton's Fig. CXXXIII *ter*. (1920, p. 286), of a young *Ichthyosporidum* in an *Acartia*, in which, however, the characteristic branching is already to be seen. This *Calanus* was sectioned and the parasite was found to have a cytological structure (see Fig. 2 C) of the kind familiar in the more or less spherical bodies always associated with developing tapeworms of both the species which are fairly common in the Clyde.[2] Figs. 2 A and B show parts of an infection of one of them for comparison with the undifferentiated parasite. Both might be compared with the figure of an older *Ichthyosporidium* (Jepps, 1937), which exhibited no movement, even under prolonged observation. It may be noted that the young worms, on the other hand, appear to be stimulated to activity by violence, and possibly by unfavourable conditions of existence. Fuhrmann (1922) says that the larvae of *Urocystis* become active on being warmed. Fig. 1 A shows what I take to be Apstein's parasite 7. He describes this and No. 6 as being "glashell" and "glasklar" respectively, and I actually overlooked (in 1933) an infection in a stage V copepodite (larva) of *Calanus* until it was stained, when spherical bodies and elongated "sausages" with swollen ends appeared, up to 200μ in length and a little over 10μ wide, and full of cells like those in the tapeworm larvae, the parasite being in a similar position but rather more anterior than in Fig. 1 A. Parasite 15 is probably a later stage of some at any rate of parasites 6–8. This probability was

[1] Quotations from my bench book.

[2] These tapeworms seem to undergo a larval development somewhat like that of *Urocystis prolifer* in *Glomeris marginata* (Coleoptera) described by Fuhrmann (1922) from the material of Joyeux; cf. also *Hymenolepis cantaniana* of Alicata & Jones (1933) in a dung beetle. No difference in the cytology of the two forms in *Calanus* was made out, and it is possible that some of these early stages might belong to yet other Platyhelminthes. I understand they are to be described in detail elsewhere.

suggested by Apstein himself in notes on his material which he handed over to Wundsch (1912, p. 7) for fuller investigation.

Parasite 9 is very scantily described and I cannot identify it. Chatton (1920, p. 309) thinks it may have been an immature spore of *Syndinium* of which I have no experience.

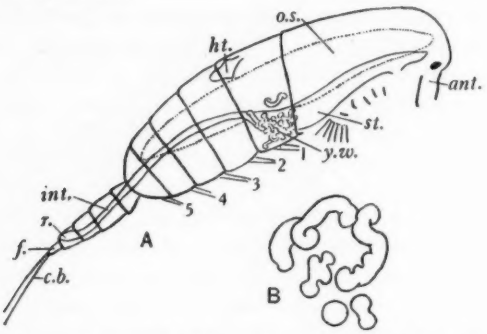

Fig. 1 A. Stage V copepodite larva of *Calanus finmarchicus* with very young Platyhelminth worms at hind end of stomach. B. Outlines of very early motile stages in development of young Platyhelminth worms, drawn from life. From body cavity of female *Calanus*. *ant.* antenna I; *c.b.* caudal bristles; *f.* furca; *ht.* heart; *int.* intestine; *o.s.* oil sac; *r.* rectum; 1–5, swimming legs; *st.* stomach; *y.w.* young worms.

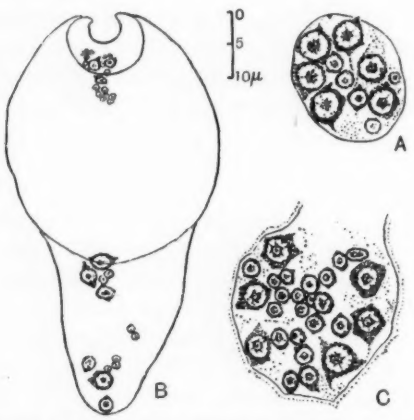

Fig. 2 A, B. From sections of *Calanus* with developing tapeworms. A, undifferentiated stage; B, differentiated larva, to same scale. Only a few cells are shown for comparison with A. Bouin, Ehrlich and eosin. Compare C, part of section of young worms shown in Fig. 1 A. Bouin, boraxcarmine and light green. Not all the cells present are shown.

Parasite 10, as Chatton points out (1920, p. 287), is for the most part almost certainly an *Ichthyosporidium*. I am rather doubtful about the "wurstartige" parasite shown in Apstein's Fig. 12 *b*, although I can suggest no alternative;

and some of his details in Figs. 12 *c–g* and in the text are not easy of interpretation. Chatton, for example, describes a stage in which the branching threads are divided up into cells, said to measure 4–5μ in diameter; but some of Apstein's "cells" look to me more like large nuclei.

Parasite 11 suggests a stage in the development of the eggs in the peculiar oviduct of *Calanus*.

Parasite 12 might be imperfectly developed or perhaps degenerating flagellispores of *Paradinium*, and so represent the end of the process begun as parasite 4. These flagellispores, normally developed outside the host, may be formed inside the *Calanus* when for any reason the *Paradinium* is not able to escape (Jepps, 1937), and in these circumstances they are often abnormal. The size given for parasite 12 fits this identification. Chatton, who believed that *Paradinium* never sporulates inside its host, considers Apstein's flagellulae as part of the life cycle of *Syndinium* or of his *Atelodinium* (1920, p. 309).

Parasites 13 *and* 14 may have been ciliates which, normally free-living, have made their way into dead or dying copepods as they so often do. Apstein seems to have felt some qualms as to the condition of the "hosts" for he says in both cases they were sometimes dead when he examined them (but cf. also Chatton & Lwoff, 1935, p. 436).

Parasite 15 resembles one of the tapeworm larvae which were common in the Clyde (see under parasites 6–8).

Parasite 16. I have never seen trematodes in the *Calanus* I have examined, but they were reported from the Clyde by Marshall *et al.* (1934).

Parasite 17. Nematodes of very different sizes were fairly common in my *Calanus* at times; as also reported by Marshall *et al.*, who had them identified as *Contracaecum* sp.

Parasite 18 is clearly not itself a parasite, but some concretions such as those found in the plasmodium of *Paradinium* at a certain stage. As Chatton, who ascribes these concretions to *Syndinium*, says, Apstein must have overlooked the actual parasite in these specimens.

Parasite 19 is *Ellobiopsis*. I do not agree with Chatton (1920, p. 388) that the distal part of the parasite shown in Apstein's Fig. 19 *b* is necessarily a cyst. It seems to me that the lines round its edge are shading intended to show up the contour as also in Fig. 19 *a*, which is certainly not encysted.

Parasite 20. No "infusorian" which could be said to cover the *Calanus* even "teilweise" has been seen by me in the Clyde specimens, but a vorticellid in this position would not be surprising. *Ephelota* has occasionally been observed, but always solitary. Several copepodite larvae of *Calanus* (stages IV and V) sent to me in formalin from Lowestoft by Mr Wimpenny had scattered over their ventral surfaces, sometimes in considerable numbers, the remarkable bodies, with a ciliate nuclear apparatus, recently described as "phorontes", an encysted stage in the life history of certain ciliates (see Chatton & Lwoff, 1935). Nothing of the kind has been found in the Clyde. As these are not ciliated however, it is not likely that they are what Apstein observed.

Parasite 21, on *Oithona*, as shown in Apstein's Fig. 20 *a*, resembles a *Paradinium* which has begun to ooze out of the anus of its host (see Jepps, 1937), and Chatton is also of this opinion (1920, p. 361). Fig. 20 *b* is hard to identify, but it must represent a product of segmentation of the plasmodium outside the host.

Parasite 22 is the ciliate I have found so frequently on the mouthparts of the Clyde *Calanus*, and I quite agree with Apstein that it is exceedingly "schlecht zu sehen". I have named it *Chattonella calani* (Jepps, 1937).

Parasite 23 from empty copepod skins seems to be a free-living dinoflagellate, perhaps a species of *Gymnodinium* as suggested by Apstein. But its frequency in this situation indicates to me, not that it is a parasite of the copepods, but that it probably has a taste for a more or less saprophytic mode of life which may be gratified by the remains of the former occupant of the skin, or merely that it seeks shelter there. (But again see Chatton & Lwoff, 1935, p. 437.)

In my opinion, then, Apstein's paper constitutes a definite record of the following parasites in pelagic Crustacea, chiefly in Copepoda, from Kiel in 1911: *Blastodinium*, Gregarines, larvae of some Platyhelminthes including definitely a tapeworm, *Ichthyosporidium*, nematodes, *Paradinium*, *Ellobiopsis*, and *Chattonella calani*.

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A NEW CYCLOPOSTHIID CILIATE (*TRIPLUMARIA HAMERTONI* GEN.N., SP.N.) PARASITIC IN THE INDIAN RHINOCEROS

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(With Plate XXIII and 1 Figure in the Text)

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Introduction

In August, 1933, I received from Colonel A. E. Hamerton, C.M.G., D.S.O., R.A.M.C. (ret.), Pathologist to the Zoological Society of London, samples of a stool obtained from an Indian rhinoceros (*Rhinoceros unicornis*) on exhibition in the Society's Gardens. The animal in question was at that time suffering from severe diarrhoea and wasting, and its faeces—preserved in 5 per cent formalin—contained numerous undetermined ciliates. On examination of the material I found that two kinds of ciliates were present, one a typical *Entodinium* (Entodiniomorpha Ophryoscolecidae), and the other an entodiniomorphous form obviously belonging to the Cycloposthiidae, but differing from all the members of this family hitherto described.

In view of this it was decided to make a special study of the cycloposthiid ciliate of which numerous specimens were available in the first sample of faeces received from the Zoological Gardens, while two further samples taken within a week after the first one contained but scanty parasites, probably owing to an improvement in the condition of the rhinoceros, as the result of treatment.

The exact localization of the ciliate in the alimentary canal of the host is unknown, but on analogy with other Cycloposthiidae living in the Perissodactyla (horse, tapir, rhinoceros) it is most probable that it inhabits the colon and/or the caecum. There is no reason to attribute the intestinal disorder to infection with this ciliate which, in common with the other Entodiniomorpha, is probably a harmless parasite. It is rather to be assumed that the appearance of large numbers of ciliates in the stools was due to their being flushed out by the diarrhoea provoked by some other cause.

The study of this ciliate, commenced in 1933, was interrupted owing to pressure of other work, and it is only quite recently that I was able to resume the investigation.

I take this opportunity to acknowledge my indebtedness to Colonel Hamerton and to the Zoological Society for placing the material at my disposal.

Methods

The structure of the new ciliate was studied in formalin preparations of specimens left unstained or tinted with Weigert's iodine, in total preparations stained with Mayer's acid haemalum and counterstained with eosin, and in sections stained by the same method.

For sections I employed Peterfi's double embedding method (Peterfi, 1921) as recommended by Strelkow (1929). Since Peterfi's publication is not easily accessible, a short description of this useful method and of the preliminary procedure adopted will not be out of place. First of all, the ciliates are separated from the coarser particles of faeces by filtration through fine gauze, after which they are concentrated by centrifugation or by sedimentation in agglutination tubes, in the course of which most of the finer faecal particles can be pipetted off. The ciliates are then stained in bulk, and passed through graded alcohols into a mixture of equal parts of 2 per cent celloidin and methyl benzoate until they are cleared (24 hours or more). In the meantime celloidin slabs are prepared by filling a Petri dish (coated with paraffin wax) to a height of 5 mm. with 4 per cent celloidin, hardening it in chloroform vapour, and cutting out slabs of the desired size. These are soaked in terpineol until they become transparent.

The ciliates to be used for sections are transferred from the celloidin-methyl benzoate mixture (with a drop of the latter) on to a cleared celloidin slab, and orientated under the microscope, after which the slab is hardened in chloroform vapour, causing the specimens to adhere to its surface. The slab is then passed through xylol to paraffin wax and embedded in the usual way.

Description

As far as I could ascertain, parasitic ciliates have never yet been recorded from the Indian rhinoceros.

Its African congener, *Rhinoceros bicornis*, harbours the following Cycloposthiidae: *Tricaudalia brumpti*, *Prototapirella clypeata*, *P. cristata*, and *Bozasella rhinocerotis* (Buisson, 1923 *a*, 1923 *b*); the systematic position of the last-named species is, however, somewhat doubtful.

Before turning to the description of the new ciliate it is necessary to say a few words regarding its orientation. In this I propose to follow Dogiel (1927) and Strelkow (1929), and to designate as the dorsal surface the one near which the macronucleus (Figs. 1–7, *ma*) occurs, the ventral surface being the one in the

region of which the anal aperture (Figs. 1, 3, *a*) lies. The anterior and posterior ends are determined by the positions of the adoral zone (Figs. 6, 7, *az*) and anus respectively. As regards the dimensions, most authors refer to the dorso-ventral diameter as breadth, which is entirely erroneous, since the correct definition of *breadth* is the measurement from side to side, whereas the dorso-ventral measurement is the *depth*. I therefore propose to refer to these dimensions according to the definition just given.

The body of the ciliate is elongated (Figs. 1, 2) and flattened laterally (Figs. 5, 7); the outline of the dorsal surface is convex, that of the ventral almost straight, the external appearance of the ciliate being somewhat similar to that of a miniature mussel. The ciliation is reduced to four groups of cirri: the adoral zone (Figs. 6, 7, *az*) and three so-called "caudals"—the anterior and posterior dorsal tufts (Figs. 1, 2, 7, *adc*, *pdc*), and the posterior ventral tuft (Figs. 1, 2, 7, *vc*).

The body is provided with a strong skeleton, in the form of a carapace, which surrounds the body on all sides, except the dorsal surface, the adoral and posterior regions (Figs. 1, 2, 4, 5). In addition to the carapace there is a dorsal skeletal rod (Figs. 1, *dt*, 2, 3, 5, *sr*) running from the anterior to the posterior end along a groove on the dorsal surface of the body (Fig. 4, *dg*).

The length of the body varies from 129·0 to 206·4μ, the depth (dorso-ventral) from 64·5 to 81·7μ, while the breadth (lateral) varies from 17·2 to 38·7μ at the dorsal surface, and from 4·3 to 17·2μ at the ventral surface, as measured at various levels in transverse and frontal sections. The transverse section of the body (Figs. 4, 5) is irregularly triangular, broadening towards the dorsal surface and narrowing towards the ventral one.

The size of the ciliate, especially its length, varies according to the age of the individual, i.e. the interval since the last division. The dimensions given above refer to "adult" individuals recognizable by the position of the micronucleus in the middle of the elongated macronucleus, whereas in "young" individuals, resulting from recent division, the micronucleus lies at one of the ends of the macronucleus.

We now turn to details of structure. The entire body of the ciliate is covered by a tough thin membrane, the pellicle (Fig. 4, *p*). The carapace—which bears a superficial resemblance to the shell of a bivalved mollusc—lies immediately beneath the pellicle and covers the ventral and both lateral surfaces of the body, its free margins bending inwards and leaving a narrow longitudinal strip of the dorsal surface uncovered (Figs. 4, 5).

The carapace is asymmetrical in shape, its right plate (Figs. 1, 2, *rsp*) being narrower but longer than the left one (Figs. 1, 2, *lsp*; 7), so that the anterior part of the right skeletal plate is visible when the ciliate is viewed from the left side (Fig. 2, *rsp*), whereas the left plate is deeper (dorso-ventrally) than the right one and can be seen when the animal is examined from the right side (Fig. 1, *lsp*).

The posterior end of the body with its two cirrose tufts (Figs. 1, 2, *pdc*, *vc*)

is only partly covered by the carapace, the posterior lateral margins of which more or less follow the configuration of this part of the body. At the anterior end both dorsal margins of the carapace are incurved in the region of the cirrose tuft (Figs. 1, 2, 7, *adc*).

The dorsal surface of the body, between the margins of the carapace, is invaginated in the form of a sunken groove—almost circular in section—which runs from one end of the body to the other and is roughly parallel to the dorsal margins of the carapace (Figs. 4, *dg*, 5, *sr*). The groove is supported throughout its length by an independent skeletal structure, the dorsal rod (=Bundle's *Leiste*, da Cunha's *lista*, de Gedoelst's *tigelle*, Hsiung's *linear skeleton*), which embraces the groove in the form of a tube with a longitudinal slit corresponding to the opening of the groove (Figs. 3, 5, *sr*). The right half of the skeletal rod extends further dorsally than the left one, on account of which the edges of the rod have the appearance of *two* more or less parallel bands when the animal is viewed from the side (Figs. 1–3, *sr*).

The right edge of the rod bears a series (about 10) of rounded denticular projections, usually visible through the right plate of the carapace (Fig. 1, *dt*).

The skeleton (carapace and dorsal rod) is composed of a single layer of numerous contiguous elements arranged perpendicularly to the surface of the body (Figs. 4, 5, *su*). When the carapace is viewed from the surface (Figs. 1, 2) it is seen that each skeletal unit is irregularly polygonal, the separate units fitting in with each other in a mozaic pattern. Each unit has a number of pore-like depressions on its outer surface. The thickness of the carapace depends upon the thickness of the above units, which is greatest in the middle of the lateral plates, gradually diminishing toward the ventral and dorsal surfaces (Figs. 4, 5). The anterior and posterior portions of the carapace also seem to be composed of smaller elements than the rest of it (Figs. 1, 2). The quasi-tubular dorsal rod is composed of similar elements, the largest being situated at its base (Figs. 4, 5). From this description it is seen that the minute structure of the skeleton of the new ciliate is similar to that in *Cycloposthium*, as described by Strelkow (1929). Like the latter it stains brown when treated with Weigert's iodine solution.

As was stated above, the ciliation of the new infusorian is limited to the adoral zone and the three "caudals". The anterior dorsal "caudal" arises between the incurved edges of the carapace (Figs. 1, 2, *adc*), to the left of the dorsal rod (Fig. 4, *adc*). The posterior dorsal "caudal" is situated on the left side of the body (Figs. 1, 2, 7, *pdc*), at a level posterior to the ventral "caudal", which occupies a more central position (Figs. 1, 2, 7, *vc*). Each "caudal" consists of a circular pad with a raised lip-like border and a central depression from which a tuft of cirri emerges (Figs. 1, 2, 3, 7, *adc*, *pdc*, *vc*). The border is not uniformly developed, so that in side-view the "pad" has the appearance of an incomplete figure of **8**. The cirri, the number of which is fairly large, can be retracted into the "pad".

The adoral zone has a complicated structure the details of which I have been unable to ascertain, owing to the imperfect fixation of the material. It consists of numerous cirri arising from a piriform body the whole of which can be retracted into a pharynx (Figs. 1–3, *ph*) occupying about one-third of the length of the body anteriorly. When everted, it is seen that the adoral zone is enclosed in a bulbous sheath, protruding beyond the anterior borders of the carapace (Figs. 6, 7, *az*). In the interior of the body there is visible a complicated system of fibrils which radiate from the pharynx to different parts of the skeleton, some of them being attached to the dorsal rod (Fig. 3, *f*). It would appear that the function of the fibrils is both to keep the buccal apparatus in position and to control its extrusion and retraction. As regards the skeletal rod, one of its roles is probably to serve for the attachment of the fibrils.

The nuclear apparatus of the new ciliate consists of one large, sausage-shaped macronucleus and a micronucleus (Figs. 1–3, *ma*, *mi*). The macronucleus is about half as long as the body: it is situated in the dorsal region of the body, on the right side, almost immediately beneath the carapace (Figs. 3, 4, 5, 7, *ma*). The micronucleus lies in a depression in the middle of the macronucleus.

There are at least six contractile vacuoles arranged in a single row along the entire left side of the dorsal region (Fig. 3, *cv*).

The anal aperture (cytopyge) is situated in the ventral region, immediately behind the base of the ventral "caudal" (Figs. 1, 3, *a*), and is connected inwards with the anal tube.

The cytoplasm of this ciliate is not distinctly subdivided into ecto- and endoplasm, but the region occupied by the nuclear apparatus is separated from the rest of the cytoplasm by a septum (Figs. 4, 5, *sp*), as in *Cycloposthium* (Strelkow, 1931 *a*).

AFFINITIES

In contrast to the other family (Ophryoscolecidae) of the suborder Entodiniomorpha, the mutual relationship between members of the Cycloposthiidae is still inadequately known. However, several genera seem to be more closely related to one another than to the other members of this family, and can be united in one group, with which the ciliate described in the present paper also appears to have affinities.

It has already been noted that the new ciliate has many features in common with *Cycloposthium*. Both have a skeleton of the same structure, the major part of which forms a carapace surrounding the body on both sides, but while in *Cycloposthium* the carapace is interrupted by ventral and dorsal grooves (Text-fig. 1 F, *vg*, *dg*), in the new ciliate it is interrupted only on the dorsal surface (Text-fig. 1 H, *dg*). The dorsal skeletal rod is of the same type in both forms; the macronucleus and contractile vacuoles are similar in appearance and in arrangement, and the cytoplasm is similarly subdivided by a septum (cf. Text-fig. 1 E, F, G, H). In fact the two types of ciliates have so much in

common that, if it were not for the presence of an additional "caudal" (anterior dorsal) in the new ciliate, the latter could be regarded as a new species of *Cycloposthium*.

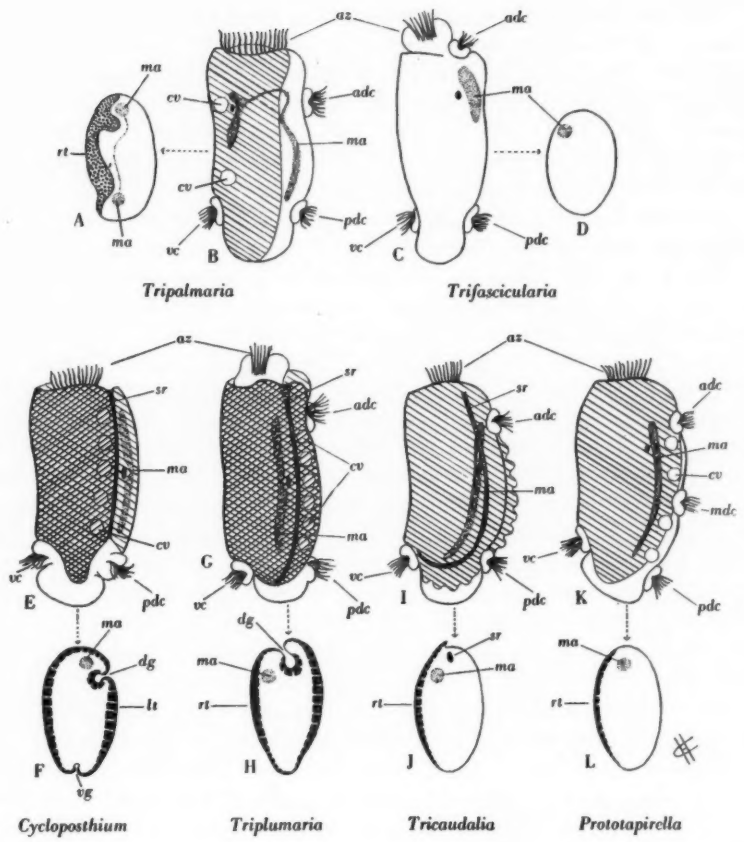
In the presence of three "caudals", similarly arranged, the new ciliate resembles *Tricaudalia*, *Tripalmaria* and *Trifascicularia*. Its likeness to *Tricaudalia* is especially pronounced, but unfortunately the description of this genus (Buisson, 1923 *a*, 1923 *b*) is so incomplete that a detailed comparison is not possible.

Tricaudalia (Text-fig. 1 I, J) possesses a skeleton in the form of a single plate on the *right* side of the body.[1] It is said to be composed of "large granulations", but the accompanying figures (Buisson, 1923 *a*, Fig. 59; 1923 *b*, Fig. 4) clearly show the same polygonal sculpture on the surface of the skeletal plate as in *Cycloposthium* and in the new ciliate, from which it may be legitimately inferred that it consists of elements similar to those in the skeleton of the other two forms. *Tricaudalia* is also provided with a skeletal rod ("tigelle"), and has an elongated macronucleus. Nothing, however, is known regarding its contractile vacuoles. The only species of this genus, *T. brumpti*, occurs in an African rhinoceros (*Rhinoceros bicornis*).

Tricaudalia undoubtedly bears a close resemblance to the new ciliate, the main difference being the reduction of its skeleton to a plate limited to one side of the body (cf. Text-fig. 1 G, H, I, J).

Before turning to the other tricaudal ciliates (*Tripalmaria* and *Trifascicularia*) it will be more convenient to consider the genus *Prototapirella*, representatives of which are found in the American tapir, African rhinoceros and elephant. This genus (Text-fig. 1 K, L) is characterized by the presence of four "caudals". A skeleton consisting of a single plate on the right side[1] was described for the African species, but no mention is made of a skeleton in the American species (*P. intestinalis*) described by Cunha (1919), who merely notes that the inner structure of this ciliate "ne se distingue pas de celle de *Cycloposthium*". In a previous description of some species of the latter genus the same author (Cunha, 1915) states that it has an alveolar layer ("camada alveolar") under the pellicle, as originally described by Bundle. From the work of Strelkow (1929) it is now known that the "alveolar layer" represents the skeleton with its characteristic polygonal sculpture. The presence of such a skeleton is clearly discernible in Cunha's figures of both *Prototapirella* and *Cycloposthium* (especially in a later paper dealing with the last-named genus: Cunha & Muniz, 1927 *a*), therefore it is fairly certain that *Prototapirella intestinalis*, like the species described by Buisson, possesses a skeletal plate on the right side. Moreover, from Buisson's figures it is evident that the minute structure of the skeleton is similar to that in *Cycloposthium*, *Tricaudalia*, and in the new ciliate. Neither Cunha nor Buisson refer to the presence of a dorsal

[1] Though Buisson (1923 *a*, *b*) orientates *Tricaudalia* and *Prototapirella* in the manner adopted in the present paper, he erroneously refers to the skeletal plate as being on the left side, whereas it is actually depicted by him on the right side.



Text-fig. 1. Diagram representing the comparative morphology of the Cycloposthiid genera: *Tripalmaria* (A, B), *Trifascicularia* (C, D), *Cycloposthium* (E, F), *Triplumaria* gen.n. (G, H), *Tricaudalia* (I, J) and *Prototapirella* (K, L). The skeleton (carapace) is shown by line shading: lines running downwards from left to right indicate skeletal plate on right side, those running upwards from left to right denote plate on left side.

B, C, E, G, I, K represent views of the ciliates from the left side; A, D, F, H, J, L show transverse sections with dorsal surface above, as viewed from anterior end (the skeletal elements are shown in black). For lettering see key to Pl. XXIII.

rod. The macronucleus and contractile vacuoles (about four in number) of *Prototapirella* have the same arrangement as in the new ciliate.

There can be no doubt that *Prototapirella* is closely related to *Tricaudalia*, differing from it in the presence of an additional "caudal" on the dorsal surface of the body (Text-fig. 1 K, *mdc*) and in the absence of the dorsal rod. It is significant that the daughter-individuals resulting from the division of *Prototapirella intestinalis* at first have only two dorsal "caudals", the third one developing later (Cunha & Muniz, 1927 *b*). It may therefore be said that *Prototapirella* passes through a *Tricaudalia* stage.

From the account given above it is seen that *Cycloposthium*, the new ciliate, *Tricaudalia* and *Prototapirella* are closely allied to each other. They all have a skeleton of the same structure, differing only in the degree of its development (cf. Text-fig. 1 F, H, J, L); an elongated macronucleus and contractile vacuoles arranged in linear order on the dorsal side (except *Tricaudalia* in which they have not been described); and "caudals" increasing in number from two to four (Text-fig. 1 E, G, I, K). The dorsal skeletal rod is a common feature in all the ciliates, except *Prototapirella*. As regards the buccal apparatus, its structure has been adequately studied only in *Cycloposthium* (Strelkow, 1929, 1931 *a*) and cannot, therefore, be compared with that in the other forms of this group.

Except for other minor differences in structure the new ciliate is like a *Cycloposthium* in which the carapace has lost the ventral fissure and has become continuous in that region, and in which an extra "caudal" is present. *Tricaudalia* may be regarded as a form like the new ciliate in which the skeleton is reduced to a single plate, while *Prototapirella* is like a *Tricaudalia* which has lost the dorsal rod, but acquired an additional "caudal" (cf. Text-fig. 1 E–L).

We can now consider the remaining two tricaudal ciliates and their relationship to what might be called the *Cycloposthium* group.

Tripalmaria (Text-fig. 1 A, B), representatives of which are parasitic in the large intestine of equines, has a superficial likeness to *Tricaudalia* in that it is provided with three similarly arranged "caudals" and has a single skeletal plate on the right side. Here, however, the resemblance ends, for in all other respects *Tripalmaria* differs not only from *Tricaudalia*, but from all the other members of the *Cycloposthium* group considered above, as is evident from the detailed description of *Tripalmaria dogieli* given by Strelkow (1931 *b*). In the first place, the skeleton of *Tripalmaria* is composed of numerous small granules embedded in a common matrix without any special orientation (Text-fig. 1 A), whereas in the *Cycloposthium* group the skeleton consists of polygonal units forming a single layer. Secondly, the macronucleus of *Tripalmaria* is arranged in an unusual manner in that it consists of two lobes, disposed on opposite sides of the body, the micronucleus accompanying the lobe which lies in the part of the body corresponding to the ventral surface of other Entodiniomorpha (Text-fig. 1 B). From the fact that during division the entire macronucleus and the two daughter-micronuclei pass over to the opposite side, where the two

"caudals" occur, it is inferred that this is the dorsal surface, as in the other Cycloposthiidae, the ventral position of the macronuclear lobe associated with the micronucleus being a secondary acquisition (Rammelmeyer, 1925; Strelkow, 1931 *b*).

Another point in which *Tripalmaria* differs from the other ciliates described above is the arrangement of the contractile vacuoles along the ventral surface (Text-fig. 1 B, *cv*). Finally, *Tripalmaria* differs from *Cycloposthium* and the new ciliate, and probably from *Tricaudalia* and *Prototapirella*, in the fact that its endoplasm is differentiated from the ectoplasm in the form of an enclosed sac. This feature is apparently absent in the Cycloposthiidae, but is characteristic of the Ophryoscolecidae (cf. Strelkow, 1931 *b*). In this and in other respects *Tripalmaria* exhibits a mixture of characters peculiar to both the families of Entodiniomorpha.

The superficial resemblance between *Tricaudalia* and *Tripalmaria* has led Cunha & Muniz (1927 *b*) to submerge the former in the latter genus, a course which was also followed by Strelkow (1931 *b*). However, as I have pointed out already, whereas *Tricaudalia* conforms in structure to the other Cycloposthiidae, the very position of *Tripalmaria* in this family is uncertain. Apart from this, the structural differences between these two genera noted above, especially that of the skeleton, the arrangement of the nuclear apparatus and of the contractile vacuoles, are sufficient to distinguish them generically. In view of this I propose to retain the original classification, with *Tricaudalia* and *Tripalmaria* as independent genera.

The last tricaudal form, *Trifascicularia* (Text-fig. 1 C, D), represented by a species parasitic in the colon of a zebra (Strelkow, 1931 *c*), differs from the other tricaudal ciliates in the complete absence of a skeleton and in the small dimensions of the macronucleus. The adoral zone in this genus (Text-fig. 1 C, *az*) is enclosed in a bulbous sheath similar to that in the new ciliate (Text-fig. 1 G, *az*). Though the affinities of *Trifascicularia* are not quite clear, it is possible, however, to regard it as a member of the *Cycloposthium* group, representing a form allied to the new ciliate (Text-fig. 1 G) and to *Tricaudalia* (Text-fig. 1 I), but in which the skeleton—already reduced to a single plate in *Tricaudalia*—has disappeared entirely.

The relationship between the members of the *Cycloposthium* group outlined above does not necessarily represent their phylogenetic history. Since nothing is known regarding the evolution of these ciliates, there is equal—if not more—justification for assuming that *Trifascicularia* is the most primitive form in this group, the other members being characterized by the acquisition and progressive complication of the skeleton, in the course of which some have retained the original number of "caudals" (*Tricaudalia* and the new ciliate), others have acquired an additional one (*Prototapirella*), while others again have lost one "caudal" (*Cycloposthium*).

Classification

From the foregoing account of the comparative morphology of some of the Cycloposthiid ciliates, it is evident that the one from the Indian rhinoceros represents a distinct form, which cannot be included in any of the existing genera. In view of this I propose to create for it a new genus, *Triplumaria* gen.n., with *Triplumaria hamertoni* sp.n. as type species, the specific name being in honour of Colonel A. E. Hamerton.

The affinities between *Triplumaria* and the other cycloposthiids have been fully discussed and are represented graphically in the accompanying text-figure.

Diagnosis

Systematic position: **Triplumaria** gen.n.

[Ciliata Spirotricha Entodiniomorpha (=Oligotrichida) Cycloposthiidae.]

Type species: T. hamertoni sp.n.

Description: In addition to adoral zone of cirri three cirrose tufts ("caudals") are present: two dorsal, one ventral. Skeleton—composed of polygonal elements disposed in single layer—consists of (1) carapace surrounding body ventrally and on both sides, leaving dorsal surface uncovered, and (2) dorsal rod, supporting longitudinal groove on dorsal surface of the body. Macronucleus elongated, sausage-shaped, accompanied by micronucleus in the middle. About six contractile vacuoles arranged in linear order on dorsal surface of the body. Dimensions: length 129·0–206·4μ; depth 64·5–81·7μ; breadth 4·3 (ventral)—38·7μ (dorsal).

Habitat: Intestine of *Rhinoceros unicornis* (Ungulata Perissodactyla Rhinocerotidae).

Locality: Zoological Gardens, London (imported from India).

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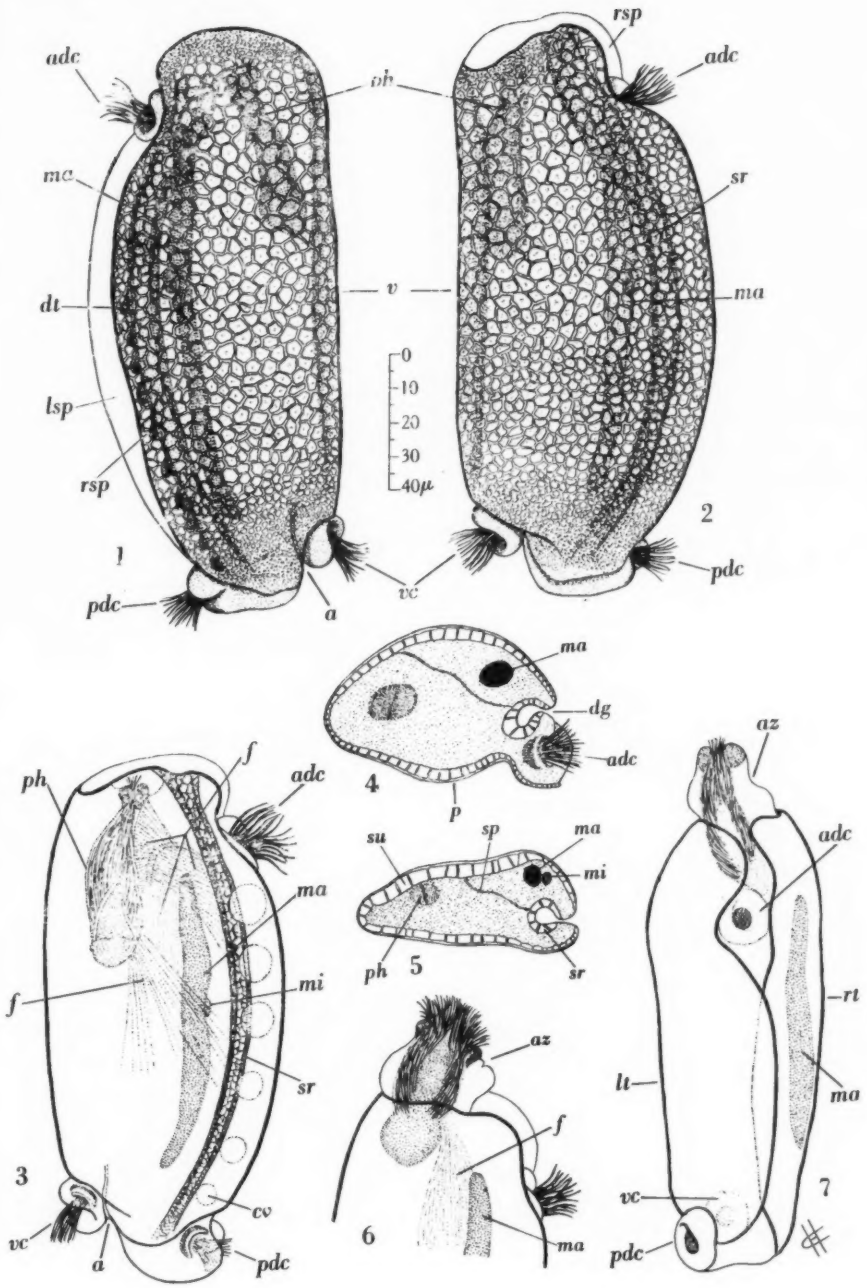
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EXPLANATION OF PLATE XXIII

(All the figures were drawn with the aid of a camera lucida at *ca.* ×500.)

Triplumaria hamertoni gen.n., sp.n.

Fig. 1. Ciliate seen from right side (adoral zone retracted).

Fig. 2. Ciliate seen from left side (adoral zone retracted).

Fig. 3. Optical longitudinal section, viewed from left side, showing dorsal skeletal rod (*sr*), six contractile vacuoles (*cv*), nuclear apparatus (*ma*, *mi*), anal aperture (*a*) and tube, pharynx (*ph*) with adoral zone and fibrils (*f*).

Fig. 4. Transverse section through the region of anterior dorsal cirrose tuft (*adc*) (view from anterior end).

Fig. 5. Transverse section through the middle of the body (view from anterior end).

Fig. 6. Anterior end of the body, showing everted adoral zone (*az*).

Fig. 7. View from dorsal surface.

Key to Lettering of Plate XXIII and Text-figure

a, anus (cytopyge). *adc*, anterior dorsal cirrose tuft ("caudal"). *az*, adoral zone of cirri. *cv*, contractile vacuole(s). *dg*, dorsal groove. *dt*, denticles on right side of skeletal rod. *f*, fibrils attached to pharynx. *lsp*, left side of carapace. *lt*, left side. *ma*, macronucleus. *mdc*, median dorsal cirrose tuft ("caudal"). *mi*, micronucleus. *p*, pellicle. *pdc*, posterior dorsal cirrose tuft ("caudal"). *ph*, pharynx. *rsp*, right side of carapace. *rt*, right side. *sp*, septum between nuclear portion and remaining cytoplasm. *sr*, skeletal rod. *su*, skeletal unit. *v*, ventral surface. *vc*, ventral cirrose tuft ("caudal"). *vg*, ventral groove.

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